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Effects of dispersal and competition with *Avena sterilis* L. on the spatial structure and dynamics of *Lolium rigidum* Gaudin in dryland cereal fields

Estructura i dinàmica espacial de *Lolium rigidum* Gaudin en conreus cerealistes de secà en relació amb els mecanismes de dispersió i amb la competència d'*Avena sterilis* L.

Memòria presentada per en José Manuel Blanco Moreno

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RESUM

1. Introducció

El coneixement de la biologia i l'ecologia de poblacions d'una espècie permet analitzar quines són les claus del seu èxit o fracàs en un ambient determinat. La dinàmica de les poblacions vegetals, és a dir, l'evolució del nombre d'individus de la població en l'espai i en el temps, és especialment atractiva des dels punts de vista teòric i pràctic quan l'objecte d'estudi són les espècies arvenses. Des d'una perspectiva teòrica, l'estudi d'espècies arvenses permet aprofundir el coneixement dels cicles vitals i l'estructura espacial. Des d'un punt de vista pràctic, el coneixement del cicle vital de les espècies arvenses, de les estratègies de regeneració de les seves poblacions i dels mecanismes de colonització de l'espai haurien de permetre el disseny de programes de control més racionals de llurs poblacions.

D'un temps ençà, s'han realitzat nombrosos treballs sobre la biologia i l'ecologia de males herbes anuals (González-Andújar & Fernández-Quintanilla, 1991; Riba Pijuan, 1993; Sans & Masalles, 1994; Fernández-Quintanilla & Sans, 1997; Sans & Masalles, 1997) i perennes (Pino *et al.*, 1997, 1998, 2002; Chamorro, 2003) a la Península Ibèrica. El motiu d'aquest interès creixent per la biologia i l'ecologia de les males herbes és justificat pel fet que són un element molt important dels agro-ecosistemes degut a que poden afectar negativament les collites. És més, si no s'emprèn cap mesura de control, les poblacions d'aquestes espècies augmenten exponencialment i poden constituir un perill encara més gran per les collites d'anys posteriors. En l'actualitat el control de les males herbes a la majoria de sistemes agrícoles es basa en l'ús d'herbicides perquè són un mitjà fiable i relativament barat. Desgraciadament, aquesta dependència sumada a l'ús (i abús) intensiu i extensiu dels herbicides (entre altres plaguicides) causa danys col·laterals al medi ambient que constitueixen una amenaça encara més gran que les males herbes. Això i l'alarma social generada pel seu impacte sobre la salut ambiental i humana ha forçat a dissenyar noves pràctiques agrícoles que tinguin en compte la reducció de l'ús d'herbicides sense provocar pèrdues excessives a les collites.

Una de les disciplines que més atenció ha merescut durant els últims temps, amb relació a la reducció de l'aplicació d'herbicides, és l'agricultura de precisió. L'agricultura de precisió, d'acord amb Pierce i Nowak (1999) és *l'aplicació de* *tecnologies i principis per a la gestió de la variabilitat espacial i temporal associada a tots els aspectes de la producció agrícola per a la millora de la producció i la qualitat ambiental*. Ara bé, l'èxit d'aquesta disciplina depèn principalment de l'avaluació i la gestió escaient en el temps i en l'espai de la variabilitat observada. No obstant els progressos recents, el potencial de millora econòmica, ambiental i social d'aquestes pràctiques resta encara lluny de ser assolit, bàsicament perquè la realitat espai–temps de la producció agrícola encara no ha estat estudiada en profunditat.

L'agricultura de precisió es justifica pel fet que els agro-ecosistemes no són espacialment homogenis i no funcionen de la mateixa manera any rera any, i la presència de males herbes no n'és una excepció. La distribució de les males herbes en rodals, descrita i caracteritzada per nombrosos equips de recerca (Coble & Mortensen, 1992; Donald, 1994; Häusler & Nordmeyer, 1995; Rew *et al.*, 1996a; Nordmeyer & Niemann, 1997; González-Andújar *et al.*, 2001a; Rew *et al.*, 2001; Wiles & Schweizer, 2002; Jurado Expósito *et al.*, 2003; Barroso *et al.*, 2004), podria ser una de les claus que conduís a una racionalització de l'ús d'herbicides. Diversos autors han conjecturat sobre els beneficis que s'obtindrien dels tractaments localitzats dels rodals i l'ajust de les dosis d'herbicida a la composició florística i a la densitat dels rodals (Dieleman *et al.*, 1999; Faechner *et al.*, 2002; Gerhards *et al.*, 2002; Jurado Expósito *et al.*, 2003).

Hi ha, però, diverses limitacions a l'aplicació generalitzada, i sovint poc crítica, de les tècniques de l'agricultura de precisió. En primer lloc, i sense afany de fer prevaler els interessos econòmics, els costos addicionals generats pel reconeixement, mesura i gestió de la variabilitat no han de sobrepassar el guany obtingut per aquestes pràctiques. En segon lloc, l'eficàcia a llarg termini d'aquestes pràctiques es pot veure afectada, entre altres, per la dispersió de llavors i l'estabilitat espacial dels rodals, així com per l'estabilitat de les relacions competitives. De manera general, els factors amb una variabilitat temporal elevada i una baixa dependència espacial seran més difícils de gestionar que aquells que presentin una forta dependència espacial i una elevada estabilitat temporal. Així doncs, la presència ben definida de rodals, l'estabilitat temporal dels rodals i l'estabilitat dels seus efectes sobre la collita representen els pilars ecològics i agronòmics sobre els quals se sostenen els principis de l'agricultura de precisió i, en conseqüència, han de ser coneguts en detall.

L'anàlisi i la modelització de la variabilitat espacial ha estat motiu de creixent interès per als equips de recerca (Wiles *et al.*, 1992; Mortensen *et al.*, 1993; Cardina *et al.*, 1995; Dieleman & Mortensen, 1999; González-Andújar *et al.*, 2001a; Rew & Cousens, 2001; Faechner & Deutsch, 2002; Wiles & Schweizer, 2002; Jurado Expósito *et al.*, 2003) perquè representen una primera passa en el disseny de mapes de tractament localitzat amb herbicides. L'anàlisi de la variabilitat espacial ha estat utilitzada bàsicament per a l'elaboració de mapes detallats a partir de mostratges grollers, per a l'establiment de bases sòlides especialment orientades a reduir i optimar l'esforç de mostratge (Wiles & Schweizer, 2002) i per a la valoració de la incertesa en els processos de presa de decisions (Wiles *et al.*, 1993; Faechner *et al.*, 2002).

Així mateix, la persistència i estabilitat temporal dels rodals és un factor decisiu en la planificació de noves tècniques de control de males herbes. Una de les qüestions fonamentals és la possibilitat de reduir els esforços de mostratge, que va lligada a la persistència dels rodals; si aquests es mantenen estables any rera any a les mateixes zones garantiria que el mapatge dels rodals d'un any seria útil per al disseny dels tractaments en anys posteriors, tot confiant que les males herbes no s'escapin de l'àrea mapada (Wilson & Brain, 1991; Gerhards *et al.*, 1997a; Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a; Barroso *et al.*, 2004).

L'anàlisi detallada de la variabilitat espacial i la seva evolució en el temps hauria de servir per facilitar la interpretació del patró de distribució espacial del organismes, dels factors ambientals i la manera com interaccionen els uns amb els altres ells. Alhora, els investigadors haurien de dirigir els seus esforços a comprendre les característiques biològiques i ecològiques de les males herbes que generen determinats patrons en rodals i a explicar les causes de l'estabilitat temporal dels rodals. La comprensió d'aquests mecanismes pot facilitar el disseny d'estratègies més dirigides a la gestió d'aspectes concrets de la variabilitat espacial de les males herbes.

Només un coneixement acurat del que succeeix en els rodals de mala herba pot permetre de dissenyar models realistes de la seva dinàmica espacial. La dispersió de llavors (Rew *et al.*, 1996b; Colbach & Sache, 2001), les tasques agronòmiques (Cardina *et al.*, 1997; Dieleman & Mortensen, 1999; Marshall & Brain, 1999; Colbach *et al.*, 2000b), i la interacció amb el medi físic (Andreasen & Streibig, 1991; Häusler &

Nordmeyer, 1995; Heisel *et al.*, 1999) i amb altres espècies (Johnson & Mullinix, 1995) són factors que afecten la dinàmica de les males herbes i que contribueixen d'una manera o altra a l'agregació de les males herbes en rodals.

Ara bé, molt sovint es tracta en termes generals de "mala herba" com un tot indiferenciat. La realitat és, però, ben diferent; les males herbes generalment formen comunitats constituïdes per diverses espècies, la composició de les quals depèn del clima, les característiques edàfiques, i la història del cultiu i la gestió que se n'hagi fet. Les comunitats arvenses són constituïdes per diverses espècies que difereixen en les seus atributs (competitivitat, mecanismes de dispersió, fenologia) i que interaccionen entre elles. En conseqüència, l'anàlisi conjunta de les diferents espècies que formen la comunitat de males herbes pot oferir una visió més realista dels patrons temporals i espacials de la seva distribució.

Però les males herbes no només interaccionen entre elles, sinó que també ho fan, òbviament, amb la planta conreada. I els resultats de la competència poden expressar-se de maneres diferents a les diverses zones d'un camp, de la mateixa manera que la collita depèn de la capacitat de retenció d'aigua, la textura del sòl, la disponibilitat de nutrients, etc. (Earl *et al.*, 2003; Taylor *et al.*, 2003). Molts plantejaments de l'agricultura de precisió es basen en l'assumpció d'un patró estable de collita (Colvin *et al.*, 1997); per tant resulta fonamental saber si les relacions competitives entre la comunitat d'arvenses i el cultiu romanen estables en el temps i en l'espai.

La variabilitat espacial i temporal dels rodals, en qualsevol cas, ha de ser convenientment tractada. Una de les prioritats és posar en relació aquesta variabilitat amb els atributs biològics de les males herbes. Entendre quins són els atributs biològics i les característiques ecològiques que més afecten la seva dinàmica pot oferir una base sòlida per al seu control. En general s'accepta que els atributs biològics que contribueixen a la inestabilitat temporal dels rodals són la manca d'un banc de llavors permanent i la capacitat de dispersió a llarga distància (Ghersa & Roush, 1993; Zhang & Hamill, 1998). Un dels factors que més importància pot tenir a l'hora de promoure la dispersió ràpida i a llargues distàncies de les llavors és la sega mitjançant segadores. Diversos autors han estudiat les segadores com a causa de la dispersió dins i entre camps (Ballaré *et al.*, 1987b; McCanny *et al.*, 1988; McCanny & Cavers, 1988; Howard *et al.*, 1991), però poques vegades s'ha relacionat les segadores amb la variabilitat espacial de les poblacions de males herbes.

L'avaluació detallada de la importància de les característiques demogràfiques (persistència del banc de llavors, patró de germinació, supervivència dels immaturs, ...), de la dispersió de les llavors i de les pràctiques de control sobre l'estructura de les poblacions i l'estabilitat espacial i temporal dels rodals contribueix a la comprensió de la dinàmica a llarg termini de les seves poblacions i pot oferir una valuosa informació que condueixi a una gestió més racional de les males herbes. Ara bé, totes aquestes informacions requereixen estudis llargs i complexos (sobre l'eficàcia dels herbicides i altres mètodes de control, sobre la interacció entre cultiu i mala herba, sobre el cicle vital de la mala herba) que molt sovint no existeix o que difícilment es pot obtenir. Una alternativa generalitzada a l'experimentació a llarg termini és l'avaluació de la dinàmica poblacional sotmesa a determinades condicions mitjançant models de simulació (Firbank & Watkinson, 1986; Ballaré *et al.*, 1987a; Perry & González-Andújar, 1993; Wallinga, 1995; Wallinga & Oijen, 1997). L'ús de models matemàtics en l'estudi de la dinàmica de poblacions permet obtenir una visió sintètica de l'evolució a llarg termini de les poblacions. D'altra banda, aquests models també permeten detectar quins són els estadis del cicle vital o les pràctiques de gestió que tenen un efecte més gran sobre les poblacions a llarg termini, i permeten dissenyar pràctiques agronòmiques que incideixin precisament en aquests estadis.

2. Objectius

El principal objectiu d'aquesta Tesi és l'estudi de l'estructura i dinàmica espacial de *Lolium rigidum* Gaudin en conreus de cereals de secà, en relació amb la competència d'*Avena sterilis* L. i amb els mecanismes de dispersió, per tal de conèixer les característiques que determinen una distribució agregada en rodals i contribueixen a generar diferències en el patró de distribució i la dinàmica espacial de les poblacions. L'estudi s'ha realitzat des de diferents aproximacions:

a) La comparació del patró espacial d' *Avena sterilis* i *Lolium rigidum* en un camp de cereals, a escales espacials contrastades, per tal de detectar quins són els factors que regulen l'evolució de l'estructura espacial del conjunt d'espècies (Capítol II).

b) La valoració de la variabilitat espacial a petita escala i entre anys de les relacions competitives d'*A. sterilis* i *L. rigidum* en comunitats arvenses de conreus de blat, mesurades en termes de reducció de la collita, mitjançant l'estudi sincrònic i diacrònic en posicions topogràfiques contrastades dins d'un mateix camp (Capítol III).

c) La valoració de l'efecte de diferents tipus de segadores sobre la dispersió de les llavors de *L. rigidum*, així com l'avaluació de la relació entre la dispersió secundària per segadores i la distribució espacial de les plàntules a petita escala (Capítol IV).

d) L'avaluació de les diferències entre les prediccions dels models espacials de dinàmica de poblacions de *L. rigidum* i les prediccions dels models que no tenen en compte l'espai; i, a més, avaluar l'efecte de diverses pràctiques de gestió de les poblacions de *L. rigidum* sobre l'evolució dels rodals en un camp prèviament no infestat (Capítol V).

3. L'elecció de les espècies

Molt sovint els estudis sobre l'estructura espacial de poblacions tenen en compte una única espècie, o tracten les diferents espècies individualment, o bé les tracten com un conjunt indiferenciat (Dieleman & Mortensen, 1999; Clay *et al.*, 2000; Jurado Expósito *et al.*, 2003); la realitat, com ja s'ha esmentat, és ben diferent. Les espècies arvenses formen en general comunitats pluriespecífiques, encara que molt sovint empobrides i poc estructurades per l'ús intensiu i sovint desaforat d'herbicides.

Entre les espècies que més sovint coexisteixen als conreus de cereals de secà de la regió Mediterrània destaquen *Avena sterilis* L. i *Lolium rigidum* Gaudin. Totes dues són gramínies anuals que creixen als conreus de secà, en general, així com en ambients lleugerament ruderalitzats (Bolòs & Vigo, 2001). Tot i que ambdues espècies són natives de la conca Mediterrània, han esdevingut males herbes molt importants arreu del Món en zones de clima mediterrani (Martin, 1996). Les dues espècies són particularment problemàtiques als conreus de cereals de secà; per aquesta raó la bibliografia referent a la interacció amb els cultius és molt abundant, però gairebé sempre les dues espècies són tractades per separat (Cousens & Mokhtari, 1998; Dhima *et al.*, 2000; Dhima & Eleftherohorinos, 2001; González Ponce & Santin, 2001; Lemerle *et al.*, 2001; Izquierdo *et al.*, 2003). L'estructura espacial de les seves poblacions no ha estat encara estudiada en detall, i solament alguns autors les han incloses en estudis més generals sobre l'estructura espacial de les males herbes (González-Andújar & Navarrete, 1995; Lamb *et al.*, 1999; Barroso *et al.*, 2004). A més, la dispersió de les llavors només ha estat estudiada en el cas d'*A. sterilis* o altres espècies del mateix gènere (González-Andújar & Perry, 1995; Shirtliffe *et al.*, 2002). Cal destacar, que sempre que ens referim a la dispersió de llavors en Poàcies, ens referim a la dispersió de fruits sencers (les cariopsis) sovint acompanyats de restes florals.

L. rigidum Gaudin (margall) és una gramínia anual que pot assolir gairebé un metre d'alçada, tot i que els individus poden ser molt variables de mida i d'aspecte. Els fillols, que molt sovint presenten a la base una coloració violàcia (antocians), un cop elongats tenen de dos a quatre nusos. En estadi de plàntula presenta les fulles inicialment conduplicades; un cop desplegades són glabres i lluents i mesuren fins a 15 × 0,8 cm. La inflorescència és una espiga fins de 30 cm, constituïda per unes 20 espiguetes dístiques que tenen de 2 a 10 flors. Les espiguetes, un cop madures, rarament es desarticulen abans de la collita, de manera que la dispersió es produeix bàsicament sota l'acció de les segadores.

L. rigidum habita erms, vores de camins i conreus d'anuals de secà, però ocasionalment també forma part de prats d'anuals o de camèfits en zones mediterrànies. Actualment és una de les males herbes més esteses en els camps de cereals de Catalunya (Recasens *et al.*, 1996) on ha esdevingut l'espècie dominant (i, de vegades, l'única), en resposta als canvis de les pràctiques agronòmiques dels camps de cereals (increment de la pressió d'herbicides, canvi a sembra directa). Diversos estudis indiquen que *L. rigidum* pot ser una mala herba extraordinàriament competitiva en conreus de cereals (Lemerle *et al.*, 1996; Lemerle *et al.*, 2001); diversos atributs biològics com són l'alta variabilitat genètica (Gill *et al.*, 1996), l'elevada producció de llavors (Monaghan, 1980; Gill, 1996a, b) i l'elevada supervivència de les llavors durant l'estiu i la tardor (Gramshaw & Stern, 1977) semblen haver contribuït al seu èxit com a mala herba i explicarien la seva persistència a llarg termini en els conreus. D'altra banda, en els últims anys diversos genotips resistents a herbicides han estat detectats arreu del Món (Matthews, 1996a), inclosa Catalunya (Taberner *et al.*, 1996).

Avena sterilis L. (cugula, cugula grossa) és també una gramínia anual, que fàcilment supera el metre d'alçada. Les fulles, majoritàriament basals, mesuren fins a 60 × 1,4 cm; les beines i marges de les fulles inferiors poden ser glabres o piloso–pubescents. La inflorescència és una panícula ampla, poc ramosa; les ramificacions terminals presenten 1 o 2 espiguetes pèndules. De cada espigueta, que pot presentar fins a 5 flors, només solen ser fèrtils les dues inferiors. Aquestes flors presenten una aresta negra llarga, colzada i retorçada fins de 8 cm de llarg. Les llavors es desprenen conjuntament, molt sovint abans de la collita del cereal.

A. sterilis habita principalment erms recents i lleugerament ruderals, vores de camins, guarets i conreus de cereals. És la mala herba més abundant i estesa a la regió central d'Espanya, així com a d'altres regions sota clima mediterrani. *A. sterilis* és una espècie molt competitiva, que redueix, fins i tot quan es presenta a baixes densitats, les collites i, amb molta menys incidència, la qualitat d'aquestes (Medd, 1996b). *A. sterilis*, així com altres espècies del gènere, com ara *A. fatua* L. i *A. strigosa* Schreb., es troben entre les males herbes més competitives dels conreus de blat (Poole & Gill, 1987; Torner *et al.*, 1991; González Ponce & Santin, 2001). Darrerament s'han detectat genotips resistents a diferents grups d'herbicides arreu del Món (Nietschke & Medd, 1996; Heap, 1997; Cavan *et al.*, 1998).

4. Patrons espacials i temporals dels poblaments mixtes de *Lolium rigidum* i *Avena sterilis* en conreus de cereals

Introducció i objectius

El coneixement de la distribució espacial de les males herbes als conreus és crucial per entendre la dinàmica espacial dels rodals, i poder establir models de dinàmica de poblacions més realistes (Cardina *et al.*, 1997). A més, la descripció acurada de la distribució de les males herbes dins dels camps de conreu pot oferir informació molt valuosa sobre els diferents factors que afecten la distribució espacial de les males herbes, com interaccionen i la importància relativa que hi tenen. Aquests factors, però, poden operar a escales molt diferents, raó per la qual resulta essencial treballar a una dimensió ajustada a l'escala del fenomen per a poder realitzar una anàlisi adequada d'aquests factors. La descripció conjunta de les diferents espècies que viuen en un mateix hàbitat permet avaluar la importància dels trets biològics de les espècies en relació a l'estructura espacial i l'evolució de les poblacions. Aquest capítol pretén: 1) conèixer l'estructura espacial a gran escala de poblaments mixtes de *L. rigidum* i *A. sterilis*; 2) avaluar l'evolució de l'estructura espacial a gran escala al llarg de tres anys consecutius; 3) relacionar la variabilitat espacial a gran escala amb els fenòmens de dispersió primària i secundària i les relacions d'interferència entre ambdues espècies; 4) posar en relació el patró espacial a petita escala d'ambdues espècies amb els mecanismes de dispersió i les pràctiques agronòmiques.

Material i mètodes

Per a l'estudi de l'estructura espacial de les poblacions a diferents escales i l'evolució de l'estructura espacial a gran escala es van realitzar dos mostratges paral·lels. A gran escala es va fer un mostratge extensiu d'un camp de blat (*Triticum aestivum* cv. Soissons) infestat predominantment per *L. rigidum* i *A. sterilis* per tal d'evitar l'efecte d'altres espècies acompanyants. A petita escala es va fer un mostratge intensiu de quatre petites parcel·les dins del mateix camp.

Les campanyes de mostratge van ser dutes a terme els hiverns dels anys 2001, 2002 i 2003 en una finca comercial d'aproximadament 8 hectàrees, situada al terme municipal de Calonge de Segarra (comarca de l'Anoia, 41º45'32" Nord 1º31'29" Est). Aquesta finca havia estat sembrada amb blat els anys anteriors i va ser sembrada també amb aquest cultiu durant el desenvolupament de l'experiència. La gestió de la finca es va deixar a l'agricultor que, amb excepció de l'aplicació d'herbicida, va operar d'acord amb la rutina habitual. Les operacions de sembra, sega i llaurada van ser efectuades en la direcció Est–Oest aproximadament, seguint les línies de mínim pendent. Les herbes dicotiledònies van ser tractades amb una barreja d'herbicides de post-emergència (clorsulfuró i metil-tribenuró) cada any. Per evitar la interferència de factors externs a la pròpia dinàmica de les males herbes, l'experiència va ser inicialment dissenyada sense graminicides; però l'important increment de la densitat de males herbes l'any 2002 ens va portar a fer un tractament amb metil-diclofop, que no va tenir grans efectes sobre la població de gramínies degut a les fortes pluges que van caure després de la seva aplicació. A més, hi ha indicis de que com a mínim la població de *L. rigidum* és resistent a herbicides inhibidors de l'acetil coenzim carboxilasa –metil-diclofop i tralkoxidim, J. Recasens i A. Taberner, comunicació personal–. Les plàntules van ser identificades i comptades cada any abans de l'aplicació d'herbicides (entre el 7 i el 31 de gener, depenent de l'any). Els recomptes van ser obtinguts als mateixos punts cada any. La relocalització va ser garantida mitjançat un sistema diferencial de localització global (DGPS, Differential Global Positioning System) Ashtech G-12 (Magellan Corporation, Santa Clara, Califòrnia, USA).

El mostratge a gran escala es va dur a terme mitjançant una malla de 16 columnes × 14 files (150 m Est–Oest × 130 m Nord–Sud) equidistants 10 m. Les densitats de totes dues herbes van ser avaluades a totes les interseccions de la malla. Degut a la variabilitat a escales inferiors al metre que presenten les poblacions, *L. rigidum* va ser comptat en nou quadrats de 10 cm de costat, situats aleatòriament dins d'una àrea d'un metre quadrat. La densitat d'*A. sterilis* va ser avaluada en 4 quadrats de 25 cm de costat dins de l'àrea d'un metre quadrat en el moment de la collita dels anys 2001 i 2002. L'any 2003 va ser comptada conjuntament amb *L. rigidum* en els quadrats de 10 cm de costat.

El mostratge a petita escala va ser realitzat en quatre parcel·les quadrades de 10 m de costat l'any 2003. Aquestes parcel·les van ser seleccionades per tenir representació d'àrees amb diferents densitats d'ambdues espècies. No obstant això, la densitat de *L. rigidum* va ser similar entre parcel·les degut a que era elevada i força homogènia a tot el camp. La presència d'*A. sterilis* era molt més localitzada al camp, i va ser possible trobar àrees amb densitats elevades i àrees amb baixa densitat. Aquestes parcel·les de 10 m de costat van ser mostrejades també en una xarxa regular, però de 21 files × 21 columnes, amb 441 punts de mostratge equidistants 0,5 metres.

Per dur a terme l'anàlisi de la variabilitat espacial tant a gran com a petita escala, les dades de densitat van ser transformades mitjançant logaritme, per evitar la forta asimetria de les dades, i se'n va treure la tendència espacial mitjançant l'algorisme del *median polish* (Cardina *et al.*, 1995). Aquest procediment, executat en una malla regular, descomposa les variables en l'efecte fila, l'efecte columna i el residu, que és el que se sotmet a l'anàlisi geostadística. La dependència espacial de les mostres es va caracteritzar mitjançant correlogrames direccionals expressats en forma de semivariograma. L'índex de correlació espacial va ser calculat tant per les dades transformades com per als residus del procés de l'algorisme del *median polish* (a partir d'ara, els residus) per avaluar l'efecte de la tendència espacial sobre les assumpcions geostadístiques. La correlació va ser calculada en quatre direccions de l'espai (0, 45, 90 i 135 graus en el sentit del rellotge des del Nord) per cada espècie i any, amb una tolerància angular mínima per avaluar el grau d'anisotropia. Els semivariogrames experimentals així obtinguts van ser ajustats a un model teòric vàlid (dos models esfèrics més la variabilitat no estructural) mitjançant el procediment dels mínims quadrats ponderats (Cressie, 1985).

L'estabilitat espacial dels rodals i les relacions espai-temps d'ambdues espècies van ser analitzades només a gran escala. L'estabilitat espacial de les poblacions de males herbes va ser caracteritzada mitjançant tres procediments diferents: el coeficient de correlació de Pearson amb les dades transformades i amb els residus; el coeficient de codispersió (Goovaerts, 1998) sobre els residus; i el test proposat per Syrjala (1996). Les relacions espacial-temporals entre les dues espècies van ser analitzades mitjançant el coeficient de correlació de Pearson amb les dades transformades i amb els residus, així com amb el coeficient de codispersió.

Resultats

Les poblacions d'ambdues espècies van evolucionar de manera diferent al llarg de l'estudi. Les dues espècies van incrementar molt les seves poblacions (tot i l'aplicació d'herbicida el 2002). Com que *L. rigidum* ja ocupava tot el camp a l'inici de l'experiència, no es va detectar una expansió dels rodals, però sí una reorganització de les zones d'alta i baixa densitat. *A. sterilis* va experimentar una forta expansió dels rodals.

A gran escala, les poblacions de les dues espècies van presentar dependència espacial, tot i que variable segons l'espècie i l'any, tant si considerem les dades transformades com els residus. La sostracció de la tendència espacial de les dades va facilitar la reducció de l'anisotropia zonal en l'estimació del semivariograma teòric i l'establiment del rang efectiu de dependència espacial. Dos models esfèrics van ser necessaris per descriure correctament l'efecte "forat" (símptoma de periodicitat) d'alguns semivariogrames experimentals (principalment a *A. sterilis*) i el ràpid increment de la semivariància a distàncies curtes. En general, *A. sterilis* va presentar una dependència espacial més forta que *L. rigidum*; la variabilitat no estructural va representar entre l'11% i el 27% de la variabilitat total (entre el 0% i el 26% en l'anàlisi duta a terme amb els residus), mentre que per *L. rigidum* va representar entre el 0% i el 53% (entre el 3% i el 60% en l'anàlisi duta a terme amb els residus). De manera general, les dues espècies van presentar un descens de la variabilitat no estructural al llarg dels tres anys.

A petita escala ambdues espècies van presentar dependència espacial a totes les parcel·les; el nivell de variació no estructural va estar per sota del 50% en gairebé tots els casos. Les dues espècies van presentar efecte "forat" i anisotropia zonal a una parcel·la o altra, però la incidència d'aquests fenòmens va ser molt més gran a *L. rigidum* que a *A. sterilis*. En general *L. rigidum* va presentar un patró de variació periòdic en la direcció perpendicular al pas de la maquinària agrícola i anisotropia zonal en la direcció paral·lela al pas d'aquesta. Segurament aquests fenòmens estan lligats a la manca d'un mecanisme de dispersió pre-collita i una forta acció de les segadores sobre la dispersió de les llavors. En canvi, *A. sterilis* no va presentar efectes "forat" clars (excepte en una parcel·la) però sí una lleugera anisotropia geomètrica, amb rangs de dependència espacial més llargs en la direcció paral·lela al pas de les segadores.

Les anàlisis d'estabilitat de les poblacions van oferir resultats contradictoris. Tot i que per *L. rigidum* cap de les proves va oferir evidències d'estabilitat espacial, per *A. sterilis* els diferents procediments van donar resultats contraposats. El test de Syrjala no va recolzar l'estabilitat espacial dels rodals que visualment s'observa, no obstant existir certa correlació entre la densitat de les poblacions d'*A. sterilis* entre anys consecutius, tant amb les dades transformades com amb els residus, element que ens indica que la correlació no es deu a l'existència de tendència espacial en les dades. El coeficient de codispersió recolza aquests resultats.

D’altra banda, el desenvolupament de les estructures espacials de totes dues espècies no és independent. Tot i que hi ha una correlació positiva (ρ = 0,306, *P* < 0,001) entre les densitats transformades de *L. rigidum* i d’*A. sterilis* el 2001, aquesta correlació desapareix en l’anàlisi amb els residus (ρ = 0,097, *P* > 0,05). Això indica que la correlació era deguda a la tendència de les dades. No obstant, es detecta una correlació negativa entre les densitats d’*A. sterilis* en qualsevol dels anys i de *L. rigidum* el 2003 ($\rho_{\mathit{L.\ rigidum}\ 2003\text{–}\mathit{A.\ sterilis}\ 2001}$ = -0,315, *P* < 0,001), i aquesta correlació roman significativa tot i la sostracció de la tendència ($\rho_{\mathit{L.\ rigidum}\ 2003\text{–}\mathit{A.\ sterilis}\ 2001}$ = -0,323, *P* < 0,001). Aquesta relació també s’observa en l’anàlisi del coeficient de codispersió. Aquest fenomen ens indica una relació antagònica entre *A. sterilis* i *L. rigidum,* on l’espècie més competitiva (*A. sterilis*) en el decurs de l’estudi, desplaça progressivament l’espècie que és inicialment més abundant.

5. Estabilitat espacial i temporal de les relacions entre males herbes i pèrdues de collita en poblaments mixtes de *Lolium rigidum* i *Avena sterilis*

Introducció i objectius

L’estabilitat de les relacions d’interferència entre les males herbes i el cultiu a diferents escales espacials (p.e. regions, camps) i temporals és la base per a l’aplicació de certes pràctiques d’agricultura de precisió i la teoria del llindar econòmic (Colvin *et al.*, 1997). Tot i això, l’estabilitat de les relacions competitives entre el conreu i les males herbes entre diferents parts d’un mateix camp no ha estat estudiada. A més, l’avaluació de l’estabilitat de les relacions competitives entre el conreu i els poblaments mixtes de males herbes que tot sovint es presenten en els cultius ha estat escassament explorada. Només en uns pocs casos s’ha analitzat l’efecte de poblaments mixtes de males herbes sobre el conreu (Hume, 1993; Pannell & Gill, 1994; Swinton *et al.*, 1994; Moechnig *et al.*, 2003), sovint en condicions experimentals i sense parar cap mena d’atenció a l’estabilitat d’aquestes interaccions. Aquest capítol pretén: 1) establir la capacitat competitiva de *L. rigidum* i d’*A. sterilis* en poblaments naturals mixtes, en un conreu de blat; 2) avaluar l’estabilitat d’aquestes relacions competitives entre posicions topogràfiques diferents dins d'un mateix camp; 3) valorar quina és l'estabilitat interanual de les relacions competitives entre aquestes males herbes i el conreu.

Material i mètodes

L'experiència es va realitzar en una finca comercial localitzada al terme municipal de Calonge de Segarra (comarca de l'Anoia, 41º45'32" Nord 1º31'29" Est) que havia estat sembrada amb blat (*Triticum aestivum* cv. Soissons) els anys anteriors i durant la realització de l'experiència. Aquest camp presentava una topografia molt irregular. Tota la finca pertany a un únic sistema de drenatge que transcorre del límit Sud-Est cap al cantó Nord-Oest; la textura del sòl varia de franca a franco-argilosa, sense diferències notables entre les diferents zones del camp. Les dades de pluviositat i temperatura obtingudes provenen de l'estació de la Xarxa Agro-Meteorològica de Catalunya més propera, a Pinós (comarca del Solsonès), a uns 7 km al Nord de la finca.

Es van delimitar tres àrees de 31 m × 51 m (a les quals s'hi farà referència en endavant com a àrees 1, 2 i 3) situades en posicions topogràfiques contrastades, amb diferències d'elevació des del punt més baix fins de 10 metres; es va procurar que aquestes àrees fossin el més planes possible, tot i que enlloc del camp hi havia àrees planes extenses. A més, aquestes àrees també diferien lleugerament en la inclinació i l'exposició. Tot i que inicialment presentaven infestacions desiguals de les dues espècies, el rang de densitats a cadascuna de les àrees era suficient per permetre les anàlisis estadístiques.

Dins de cada àrea es van establir 24 quadrats de mostratge d'1 m de costat, equidistants 9 m en una malla regular. Aquestes unitats van ser georeferenciades amb un DGPS Ashtech G-12 (Magellan Corporation, Santa Clara, Califòrnia, USA) per garantir la localització exacta cada any. La densitat de males herbes va ser mostrejada a l'hivern (7 i 8 de gener de l'any 2001, i 30 i 31 de gener de l'any 2002). *L. rigidum* va ser recomptat en nou quadrats de 10 cm de costat situats a l'atzar dins de les unitats de mostratge; *A. sterilis* va ser comptada en 4 quadrats de 25 cm de costat degut a la densitat més baixa i la mida més gran de les plàntules. La biomassa (collita) de blat va ser recollida a la maduresa del conreu (7 de juliol del 2001 i 10 de juliol del 2002) en 4 marcs de 25 cm de costat.

Per poder calcular les pèrdues de rendiment degudes a les males herbes es van fer mesures del rendiment potencial del blat en aquestes àrees. La collita sense mala herba es va calcular a partir de 6 quadrats de 0,5 m de costat, disposats regularment dins de cada àrea. Aquestes unitats van ser desherbades mitjançant l'aplicació de metil-diclofop a dosi de 712 g.i.a. ha^{-1}. El segon any, degut a fortes pluges després de l'aplicació, l'herbicida no va tenir l'efecte desitjat; per això es va establir el nivell de potencialitat com el nivell màxim de collita trobat en les unitats de mostratge amb les infestacions més baixes de males herbes i la màxima biomassa de cereal (Jasieniuk *et al.*, 1999).

La relació entre la densitat de males herbes i les pèrdues de collita va ser descrita mitjançant la modificació proposada per Swinton *et al.* (1994) del model hiperbòlic proposat per Cousens (1985):

$$\textit{pèrdua de collita} = \frac{\sum_i I_i w_i}{1 + \sum_i I_i w_i / A} \qquad (1)$$

on w_i és la densitat de l'espècie *i*, el paràmetre I_i és el pendent inicial de l'efecte de l'espècie *i* i *A* és la pèrdua màxima de collita a densitats elevades de mala herba.

Les corbes de competició van ser estimades mitjançant el procediment de regressió no lineal. Quan la regressió no era significativa les corbes van ser excloses de les anàlisis subsegüents, però si eren significatives i la variància de l'error era constant entre àrees, les corbes obtingudes van ser comparades pel procediment de la suma de quadrats extra (Ratkowsky, 1983; Lindquist *et al.*, 1996). Aquest procediment permet detectar si els paràmetres estimats són diferents per a cada àrea i any, és a dir, si els efectes de *L. rigidum* (I_r) i d'*A. sterilis* (I_o) són els mateixos entre àrees i anys; i si les pèrdues totals (*A*) produïdes pels poblaments mixtes d'*A. sterilis* i *L. rigidum* són constants entre àrees i anys. La comparació entre corbes va ser efectuada primer entre àrees dins de cada any, i després entre anys, degut a que la variabilitat espacial a petita escala és plausible que sigui més petita que la variabilitat interanual (especialment en ambients on la variabilitat interanual pot ser molt gran, com als ambients mediterranis). Si els paràmetres de les corbes no són significativament diferents entre àrees, les dades poden ser tractades conjuntament per comprovar l'estabilitat dels paràmetres entre anys.

Resultats

A l’àrea 3 no hi va haver cap relació entre la densitat de males herbes i les pèrdues de collita; per aquesta raó aquesta àrea va ser exclosa de les anàlisis subsegüents. A les àrees 1 i 2 la relació hiperbòlica entre la densitat de males herbes i les pèrdues de collita va ser significativa els dos anys ($P < 0{,}0001$). No obstant, la bondat d’ajust del model descrit va ser força diferent entre anys i entre àrees. L’ajust va ser millor per a l’àrea 1 el primer any (R^2 ajustada = 0,6125) que el segon (R^2 ajustada = 0,20086), mentre que a l’àrea 2 l’ajust va ser millor el segon any (R^2 ajustada = 0,65387) que el primer (R^2 ajustada = 0,38419).

Com que la regressió va ser significativa i la variància de l’error va ser constant entre àrees, es van comparar les corbes de competència entre àrees dins d’un mateix any. Els resultats de la suma de quadrats extra indiquen que ni l’efecte competitiu de *L. rigidum*, ni l’efecte competitiu d’*A. sterilis*, ni les pèrdues de collita màximes van ser diferents a petita escala, tot i que la collita potencial va ser diferent entre les diferents àrees del camp.

Atès que no es va detectar variabilitat espacial cap dels dos anys en els paràmetres estimats, les dades d’ambdues àrees van ser analitzades conjuntament per provar l’estabilitat interanual dels paràmetres de competència. El procediment de la suma de quadrats extra indica que es mantenen constants entre anys l’efecte competitiu d’*A. sterilis* i les pèrdues màximes de collita; això vol dir que aquests paràmetres són poc variables en funció de les condicions ambientals. L’efecte competitiu de *L. rigidum* varia entre anys, la qual cosa indica que les condicions ambientals modifiquen la seva capacitat de competir amb el blat. *L. rigidum* va ser molt menys competitiu el segon any que el primer. D’altra banda, *L. rigidum* va ser menys competitiu que *A. sterilis* a totes les àrees i tots dos anys; es pot, doncs, entendre que és un competidor més feble que no pas *A. sterilis*, fins i tot a densitats molt elevades.

6. Distribució espacial de les plàntules de *Lolium rigidum* deguda a la dispersió per segadores

Introducció i objectius

La distribució espacial de les males herbes als conreus està relacionada amb nombrosos factors, entre els quals hi ha l'acció de la maquinària agrícola sobre la dispersió de les llavors. L'efecte d'aquests factors agronòmics ha de ser quantificat per poder millorar les prediccions de l'evolució de la mida de les poblacions de males herbes (Rew *et al.*, 1996b; Paice *et al.*, 1998; Wallinga *et al.*, 2002). La modelització matemàtica de la dispersió de llavors pot ser utilitzada per predir les taxes d'expansió de les males herbes, així com per explicar les causes de l'heterogeneïtat de les poblacions de males herbes, i suggerir les implicacions que això té per a la gestió de les seves poblacions (Woolcock & Cousens, 2000). El present estudi pretén: 1) avaluar la contribució de dos tipus de màquines segadores –estàndard i amb picadora de palla– sobre la dispersió de les llavors de *L. rigidum*; 2) examinar l'efecte d'aquestes màquines sobre el patró de distribució de les llavors de *L. rigidum*; 3) descriure el patró espacial de les poblacions de *L. rigidum* a petita escala i posar-lo en relació amb el tractament de la palla que fan les segadores.

Material i mètodes

Per a l'estudi de l'efecte de les segadores sobre la dispersió de llavors es va realitzar una experiència en una finca comercial d'ordi a la localitat de Concabella (els Plans de Sió, comarca de la Segarra, 41º40'51" Nord 1º20'6" Est); aquesta finca inicialment no presentava infestacions de *L. rigidum*. Es va dissenyar una experiència d'una factor, el tipus de segadora, i tres rèpliques. Es van delimitar tres parcel·les (rèpliques) dins de cadascuna de les quals es van establir dues subparcel·les, una de les quals va ser segada amb la segadora estàndard (Deutz Fahr 3578H) amb una amplada de tall de 4,80 m, i l'altra amb la mateixa màquina però acoblant-hi el mecanisme de picar i esbargir la palla. Al mig de les subparcel·les es van establir, mitjançant sembra, sengles rodals de 4 m × 5 m a una densitat de 6000 llavors m^{-2}. Immediatament després de la sega es van recol·lectar mostres múltiples cada 3 m en el sentit de la marxa de la segadora des de 9 metres per darrera del centre del rodal fins a 18 m per davant d’aquest. Les cinc submostres que composaven cada mostra múltiple es van prendre perpendicularment al sentit de la marxa, una centrada amb l’eix de la segadora y dues a cada costat separades per un metre. A cada submostra es va recol·lectar dins de quatre marcs de 10 cm de costat tot el material vegetal dipositat a la superfície del sòl. El recompte de les llavors de cada submostra es va fer per germinació en condicions d’hivernacle.

La redistribució de les llavors en la direcció de la marxa de la segadora va ser ajustada a una funció composta per una funció normal i una exponencial negativa, que descriuen respectivament l’alliberament en massa de la majoria de les llavors poc després de ser recollides per la segadora (el paràmetre μ d’aquesta funció representa la posició de l’alliberament en massa) i la lenta deposició de llavors que estan sent processades per la segadora (el paràmetre β representa l’invers de la taxa d’alliberament de llavors, i implica la capacitat de transport longitudinal de les llavors). La redistribució en la direcció perpendicular va ser descrita per una funció de Cauchy centrada en l’eix de la segadora; el paràmetre de forma *s* d’aquesta funció representa el grau de concentració de les llavors amb el residu –palla i goll– de la collita.

L’ajust de les funcions va ser realitzat mitjançant regressió no lineal per mínims quadrats. La comparació entre segadores va ser portada a terme mitjançant l’aproximació de variables indicadores (Neter *et al.*, 1990), que permet testar directament si la diferència entre els paràmetres estimats per cada tractament és significativament diferent de zero.

La descripció i l’avaluació de la relació entre el patró de deposició de la palla després de la sega i la distribució de les plàntules de *L. rigidum* va ser portada a terme en una altra finca. Es va seleccionar un camp de blat (*Triticum aestivum* cv. Soissons) amb elevada infestació natural de *L. rigidum* al terme de Calonge de Segarra (comarca de l’Anoia, 41º45’32” Nord 1º31’29” Est). Es van seleccionar quatre parcel·les de 10 m × 10 m per tenir representació d’àrees amb diferents densitats. Es va fer un seguiment de la deposició de la palla i la densitat de *L. rigidum* seguint una xarxa regular de 21 files × 21 columnes, amb 441 punts de mostratge equidistants 0,5 metres. Aquestes parcel·les van ser mostrejades l’estiu del 2001, l’hivern i l’estiu del 2002 i l’hivern del

2003. La presència de palla es va avaluar després de la sega en forma de dades binàries (presència o absència) i les plàntules de *L. rigidum* van ser comptades en marcs de 10 cm de costat. En les anàlisis només se'n van emprar les dades de tres de les parcel·les perquè una de les parcel·les era molt a prop del marge del camp i la segadora va passar dues vegades per sobre de manera que la presència de la palla no corresponia amb la deposició original.

Les relacions entre la deposició de palla i la densitat de plàntules de *L. rigidum* es va realitzar mitjançant l'anàlisi de la semivariància de dades binàries (*indicator semivariance*), autosemivariància si s'analitza només una de les dues variables i semivariància creuada si s'analitzen les dues variables alhora. Aquesta anàlisi es va utilitzar per descriure el grau de dependència espacial de les variables (presència de palla i densitat de *L. rigidum*) i el grau de dependència espacial entre elles ($\text{palla}_{\text{any0}}$–$\text{palla}_{\text{any1}}$, $\text{palla}_{\text{any0}}$–$\text{plàntules}_{\text{any1}}$, $\text{plàntules}_{\text{any0}}$–$\text{plàntules}_{\text{any1}}$).

Resultats

Les màquines segadores tenen un paper molt important en la dispersió de les llavors de *L. rigidum*. Les segadores poden transportar les llavors de *L. rigidum* fins als 18 m en el sentit de l'avenç; a més hi ha una fracció important de les llavors que són propulsades enrera, especialment en la segadora amb picadora. La presència de llavors a les mostres més allunyades del rodal indica que la dispersió pot arribar a distàncies encara més llargues. La dispersió de *L. rigidum* per segadores és superior a la d'espècies del gènere *Bromus* (Howard *et al.*, 1991), però no tan eficient com a *Panicum miliaceum* L. (McCanny & Cavers, 1988), les llavors del qual poden arribar a distàncies superiors a 50 m. Les diferències entre espècies poden ser explicades per la diferent fenologia de les espècies i per la mida de la cariopsi. Les espècies del gènere *Bromus* retenen poques llavors en el moment de la collita i són llavors grosses, i en conseqüència ràpidament expulsades per les segadores. *P. miliaceum* també reté poques llavors en el moment de la collita, però les seves llavors són més petites i en conseqüència poden quedar retingudes a la maquinària amb facilitat. *L. rigidum,* en canvi, reté la majoria de les llavors fins al moment de la sega, de manera que moltes d'aquestes llavors són dispersades per les segadores.

Els dos tipus de segadores presenten un patró de redistribució de les llavors similar, amb una acumulació màxima de llavors propera al focus. La posició de la màxima acumulació varia significativament en funció de la segadora (μ = 0,059 per a la segadora estàndard i μ = -1,277 m per a la segadora amb picadora). L'acumulació de la major part de les llavors molt a prop del focus indica que l'acció de les segadores té poca importància per a l'estabilitat dels rodals. No obstant, tot i que no hi ha diferències significatives entre màquines (β = 7,445 per a la segadora estàndard i β = 3,124 per a la segadora amb picadora), la taxa d'alliberament de llavors a mesura que avança la segadora condiciona fortament l'expansió dels rodals. Com que aquesta taxa d'alliberament de llavors és relativament baixa, es produeixen llargues esteles de llavors, que impliquen una forta expansió dels rodals.

La dispersió en la direcció perpendicular al moviment de les segadores és força limitada. La redistribució lateral a totes dues segadores produeix una acumulació de llavors sota la línia central. Però existeixen diferències entre les dues segadores; la distribució de les llavors de la segadora amb picadora és menys apuntada i amb més llavors dispersades cap als costats (s = 0,455 per a la segadora estàndard i s = 0,694 per a la segadora amb picadora). Com que la diferència entre un i altre tipus de segadora rau en el processament que fan de la palla, aquesta diferència en la redistribució de llavors indica que hi ha una fracció important de les llavors que és dispersada amb la palla.

Pel que fa a l'estructura espacial a petita escala, podem afirmar que la deposició de palla i la densitat de *L. rigidum* es correlacionen tant en la direcció del moviment de les segadores com en la direcció perpendicular a l'anterior. Totes dues variables presenten un patró comú de variació, amb una pauta gradual d'increment de l'autosemivariància en la direcció paral·lela al moviment de les segadores, i una pauta periòdica, amb pics cada 4 m, en la direcció perpendicular. A més, la semivariància creuada entre la presència de palla i la densitat de plàntules de *L. rigidum* presenta els mateixos patrons de variació, gradual i periòdic, tot indicant que realment totes dues variables, presència de palla i densitat de *L. rigidum*, comparteixen l'estructura espacial, i per tant una causa comuna.

7. Modelització de la dinàmica espacial de *Lolium rigidum* en camps de cereals

Introducció i objectius

Els estudis de dinàmica de poblacions de males herbes que es basen en densitats mitjanes no poden explicar la dinàmica espacial de les poblacions (van Groenendael, 1988; Wallinga, 1995). A més, les prediccions poden ser molt diferents de les realitzades sense tenir en compte la component espacial. Diversos processos, com ara la dispersió de llavors, la dinàmica intrínseca de les poblacions, i la denso-dependència i la component estocàstica en els processos demogràfics i de dispersió influeixen sobre la dinàmica i l'estructura espacial de les poblacions de males herbes. En aquest treball s'ofereix una visió sintètica dels efectes de la dispersió, dels processos denso-dependents i l'estocasticitat demogràfica i de dispersió sobre la dinàmica i l'estructura de poblacions de *Lolium rigidum*, una mala herba anual molt abundant en els camps de cereals del Nord-Est de la Península Ibèrica amb un banc de llavors no persistent, mitjançant un procés de simulació basat en el cicle vital i les característiques de la dispersió. Aquest estudi pretén establir: 1) fins a quin punt els models no espacials de dinàmica de poblacions ofereixen una mesura fiable de la dinàmica de *L. rigidum*; 2) quina és la taxa d'expansió de *L. rigidum* en els camps de cereals i si aquesta taxa depèn de la gestió que se'n faci; 3) quines implicacions té la gestió sobre l'estructura espacial de *L. rigidum*.

Mètodes

Estructura del model

Per conèixer l'efecte del canvi dels paràmetres demogràfics, de les diferents pràctiques de gestió i el comportament estocàstic dels processos demogràfics, es va dissenyar un model espacial basat en un model del cicle vital de *L. rigidum* publicat per González-Andújar i Fernández-Quintanilla (2004). En aquest model es van incloure, amb algunes modificacions, els processos de dispersió de llavors, tant primària (barocora) com secundària (per l'acció de la segadora), caracteritzats per Blanco-

Moreno *et al.* (2004). D’altra banda, també es va incorporar l’efecte estocàstic en els processos demogràfics segons l’aproximació de Perry i González-Andújar (1993).

Totes les simulacions van ser portades a terme en un “camp” homogeni quadrat de 50 m × 50 m, dividit en cel·les de 0,5 m × 0,5 m (10201 cel·les en total). Les plantes no van ser tractades individualment sinó que van ser sumades i assignades en grup a la coordenada del centre de la cel·la a la qual corresponen. El procés de simulació va ser iniciat amb 10 plàntules en la cel·la central –coordenades (0,0)–, a partir de les quals es calculen els adults. La producció de llavors a la cel·la és calculada a partir de la densitat d’adults i de la seva fecunditat, que és una funció depenent de la seva densitat. A partir de la producció de llavors es calcula la quantitat que queda disponible per a la dispersió després de les pèrdues per predació. Les llavors que hi romanen són dispersades mitjançant la generació d’un conjunt aleatori de distàncies d’acord a la distribució de freqüències descrita per Blanco-Moreno *et al.* (2004), que són les que defineixen, junt amb la posició de la cel·la de la planta mare, a quina cel·la han de ser incorporades. Un cop a la cel·la de destí, aquestes llavors s’incorporen al banc de llavors, a partir de les quals s’originarà la població de plàntules de la següent iteració del model de simulació.

Simulacions

En aquest model s’inclou l’efecte de diverses pràctiques de control i que regulen d’alguna manera o altra els processos demogràfics de *L. rigidum*. Les diferents tàctiques de control simulades en el model són l’endarreriment de la sembra (que redueix el percentatge efectiu de llavors del banc que s’estableixen com a plàntules); l’efecte de l’establiment de conreus competitius o amb elevada densitat i l’acció subletal dels herbicides (que redueixen la fecunditat dels individus); i la captura de llavors en el procés de collita mitjançant segadores (que redueix la quantitat de llavors que arriben a incorporar-se al banc de llavors). D’altra banda, el cicle convencional de cereal continu pot patir una disrupció mitjançant la intercalació d’un any de guaret, que degut al règim de llaurades redueix molt el percentatge de plàntules que arriben a l’estadi adult i trenca el cicle d’expansió dels rodals degut a que no hi ha l’acció de les segadores sobre les llavors.

El valor dels diferents paràmetres del model utilitzats a les simulacions va ser obtingut a partir de diferents treballs publicats sobre la biologia, el control i els mecanismes de dispersió de *L. rigidum* (Matthews, 1996b; Matthews *et al.*, 1996a; Taberner, 1996; Walsh, 1996; Fernández-Quintanilla *et al.*, 2000; Navarrete *et al.*, 2000; Walsh & Parker, 2002; Izquierdo *et al.*, 2003; Monjardino *et al.*, 2003; Blanco-Moreno *et al.*, 2004; González-Andújar & Fernández-Quintanilla, 2004). Cada combinació de paràmetres es va simular 5 vegades per tal de conèixer la variabilitat dels resultats. Els valors corresponen a la mitjana de les 5 simulacions. Les simulacions van ser iterades 30 vegades (corresponent a 30 anys a partir de la colonització) sense variació en els valors dels paràmetres entre iteracions.

La sensibilitat del model al canvi en el valor dels paràmetres va ser calculada mitjançant el mètode establert per Pannell (1997). Aquest autor proposa calcular la sensibilitat del model com la diferència entre la resposta del model amb el valor màxim del paràmetre i la resposta del model amb el valor mínim que pot prendre el paràmetre, estandarditzada per la resposta del model amb el valor màxim del paràmetre (és a dir, el grau de variació que hom pot esperar dins dels límits establerts per la variació del valor del paràmetre). La sensibilitat del model va ser calculada per a la variació de la densitat d’equilibri.

Resultats

Els resultats dels processos de simulació indiquen que la població creix seguint una corba sigmoide, però la mida de les poblacions requereix molt més temps per estabilitzar-se que no pas allò que prediu un model no espacial. Així mateix, el model espacial prediu, per un temps determinat, densitats de població més baixes que el no espacial mentre no s’arriba a la densitat d’equilibri. La densitat d’equilibri depèn de les pràctiques de control imposades en el cicle vital de *L. rigidum*, però no del procés de dispersió. Només a fecunditats molt baixes (i per tant a densitats de població molt baixes), l’efecte conjunt del comportament estocàstic de la població i la dispersió de les llavors afecta de manera substancial la densitat d’equilibri de la població. La densitat de població es manté per sota del nivell predit pel model no espacial, amb un comportament erràtic i acíclic (caòtic), sense un increment acusat de l’àrea ocupada.

La densitat de població sense cap mesura de control imposada en el cicle vital és de 2318,65 llavors m^{-2}; aquests nivells de població són molt elevats i poden causar importants pèrdues de collita si no són convenientment gestionats. La sensibilitat del model de simulació a la variació dels diferents paràmetres demogràfics és diversa. Només aquells paràmetres que actuen directament sobre la producció de llavors (fecunditat) o les pèrdues de llavors abans de la seva incorporació al banc de llavors (pèrdues per predació) repercuteixen de manera significativa en la mida de les poblacions a llarg termini. La germinació i l'establiment de les plàntules tenen un efecte molt limitat sobre la mida de la població, ja que l'efecte de la variació d'aquests paràmetres es veu àmpliament compensada per la resposta, depenent de la densitat, de la fecunditat dels individus.

L'efecte de les diferents pràctiques de gestió de les poblacions de *L. rigidum* tenen també resultats diversos segons a quina part del cicle de *L. rigidum* afectin. Algunes de les tàctiques de control imposades individualment en el model provoquen reduccions importants de la mida de les poblacions (aplicació d'herbicides: 90.9%; establiment de cultius competitius: 52.4%; captura de llavors: 57.8%). La sembra tardana, però, falla en el seu objectiu final, que és reduir el banc de llavors abans de la sembra (es produeix un increment del 3.58%) tot i que resulta efectiva en la reducció de la població de plantes que s'estableixen i competeixen amb el cultiu, de manera que es redueixen les pèrdues de collita. L'establiment d'un cicle de rotació biennal entre guaret i cultiu del cereal fa que també es doni una important reducció del banc de llavors durant l'any de guaret. Això minimitza les pèrdues del conreu de l'any següent, però durant l'any de cereal, si no hi ha control de les poblacions de *L. rigidum*, es produeix un gran increment dels efectius.

La combinació de diferents tècniques de gestió de les poblacions de *L. rigidum* resulta més beneficiosa que l'aplicació de tècniques individuals. Per exemple, l'establiment d'una estratègia on es combinin els herbicides a mitja dosi, la sembra tardana, els conreus competitius i la captura de llavors durant la collita, pot reduir les poblacions de *L. rigidum* en un 95.14%. La combinació només de mètodes culturals, com ara el cicle biennal de guaret més la sembra tardana més l'establiment de conreus competitius, poden reduir un 92.2% les poblacions de *L. rigidum* segons els resultats del nostre model.

Tot i això, totes les pràctiques es mostren poc o gens efectives en la restricció de l'expansió de la població de *L. rigidum*. L'ocupació completa del camp es dóna en un període entre 14 i 20 anys per totes les pràctiques individuals de gestió, excepte l'establiment d'un cicle biennal guaret i cereal. Aquest cicle biennal endarrereix l'expansió del rodal de *L. rigidum* degut a que durant l'any de guaret no hi ha la dispersió a gran distància de les segadores i perquè a més la població en cel·les amb pocs individus sovint s'extingeix. Els programes integrats de gestió de les poblacions de *L. rigidum* també limiten en certa mesura l'expansió del rodal, encara que no eviten la completa infestació del camp amb el temps.

8. Conclusions generals

A continuació s'enuncien les principals conclusions d'aquest treball, que s'han fet explícites a les discussions en anglès dels diversos capítols de la Tesi. De manera general, la gestió espacial i temporal de la variabilitat de poblaments mixtes de *Lolium rigidum* i *Avena sterilis* en conreus de cereals té un gran potencial d'aplicació pràctica. No obstant, determinades característiques de l'estructura espacial de les poblacions, de les relacions competitives amb el conreu i dels mecanismes de dispersió podrien suposar un obstacle a l'hora d'aplicar tècniques d'agricultura de precisió amb garantia per a totes dues espècies. Les dues espècies tenen patrons fenològics i atributs del cicle vital diferents, i això comporta que les possibilitats d'una gestió de precisió siguin diferents per a cadascuna d'elles.

1–L'anàlisi de la distribució espacial d'una mala herba en una comunitat arvense en un determinat moment i escala no ofereix una explicació de la seva estructura i dinàmica espacial. L'anàlisi de l'estructura espacial a diferents escales, de l'estabilitat espacial dels rodals, i l'anàlisi conjunta de les principals espècies d'una comunitat arvense poden ajudar a superar algunes de les deficiències dels estudis atemporals monoespecífics.

2–L’estructura de les poblacions de *L. rigidum* i *A. sterilis* a gran escala és diferent de la que presenten a petita escala; això indica que els factors que incideixen sobre l’estructura espacial de les poblacions varien en funció de l’escala.

3–*A. sterilis* mostra una estructura espacial constant a escala de camp sencer amb rodals ben definits i estables. Aquestes característiques constitueixen una base sòlida pel disseny de tractaments localitzats de les seves poblacions en camps de cereals. En canvi, l’estructura espacial de les poblacions de *L. rigidum* és poc definida i temporalment inestable. Aquestes característiques suposen un obstacle seriós pel disseny de tractaments localitzats de les seves poblacions.

4–*A. sterilis* pot reemplaçar *L. rigidum* en poblaments mixtes de camps de blat si no hi ha l’aplicació d’herbicides. En aquells llocs on les poblacions d’*A. sterilis* persisteixen al llarg dels anys poden arribar a substituir les de *L. rigidum*, degut a que la capacitat competitiva d’*A. sterilis* és més gran que la de *L. rigidum*.

5–L’efecte competitiu de *L. rigidum* sobre la collita del blat és estable dins d’un camp, independentment de la posició topogràfica. No obstant, la capacitat competitiva de *L. rigidum* pot variar molt entre anys consecutius, en funció de les condicions ambientals durant l’estació de creixement. L’efecte competitiu d’*A. sterilis* sobre la collita del blat és estable entre posicions topogràfiques així com entre anys dins d’un mateix camp.

6– *A. sterilis* és més competitiva que *L. rigidum* enfront del conreu, i aquesta relació es manté estable entre anys i entre posicions topogràfiques. La marcada estabilitat de la competitivitat d’*A. sterilis* fa que sigui més adequada per a un escenari d’agricultura de precisió que no pas *L. rigidum*.

7–Les segadores poden transportar les llavors de *L. rigidum* a llargues distàncies (més de 18 m), encara que aquest fenomen es poc rellevant per a l’estabilitat dels rodals, perquè la distància modal és propera a zero metres independentment del tipus de segadora (estàndard o amb picadora de palla) que s’utilitzi per a la sega del cereal. Els rodals no es desplacen per l’acció de les segadores. No obstant això, el moviment a llarga distància d’algunes llavors afavoreix l’extensió dels rodals i, en conseqüència, la infestació de camps sencers.

8–La forma de les corbes de dispersió per l'acció de les segadores permet suposar que l'expansió dels rodals de *L. rigidum* té lloc mitjançant un front tancat que es mou amb una taxa anual constant, sense l'aparició de poblacions "filles" aïllades.

9–La dispersió de les llavors de *L. rigidum* per les segadores comporta l'aparició d'un patró espacial periòdic a petita escala. Les segadores redistribueixen una part de les llavors de *L. rigidum* barrejades amb el goll i la palla de manera que es genera un patró en bandes paral·leles de plàntules, amb una alternança de bandes d'elevada i de baixa densitat que sovint es pot observar en els camps de cereals. Les llavors d'*A. sterilis* no es dispersen amb les segadores degut a que la majoria de les llavors s'han incorporat al banc de llavors abans de la collita del cereal; en conseqüència les seves poblacions no presenten cap patró en bandes paral·leles a petita escala.

10–La llaurada i el banc de llavors residual d'anys anteriors no afecten de manera important l'estructura espacial de les poblacions de *L. rigidum,* com demostra la forta concordança espacial entre la deposició de la palla durant la collita i la densitat de plàntules.

11–La gestió dels residus de la sega té un gran potencial per al control de les poblacions de *L. rigidum* en camps de cereals. La captura del goll amb mecanismes especialment dissenyats pot constituir una bona estratègia per reduir la quantitat de llavors que s'incorporen al banc i, en conseqüència, reduir la formació d'àrees d'elevada densitat, que afavoreixen la persistència dels rodals, tot i l'aplicació d'herbicides. No s'ha d'oblidar, però, que hi ha una fracció important de llavors que són dispersades amb la palla i per tant no poden ser controlades mitjançant la captura del goll.

12–La incorporació de la component espacial als models demogràfics de dinàmica de poblacions de *L. rigidum* no afecta la densitat d'equilibri. En canvi, els models no espacials de dinàmica de poblacions tendeixen a sobreestimar sistemàticament la densitat mentre no s'assoleix la densitat d'equilibri. Els models no espacials prediuen taxes de creixement de població més elevades en no tenir en compte la migració de llavors entre zones d'un mateix camp.

13–El model de dinàmica espacial prediu una elevada variabilitat de la població de *L. rigidum* en l'espai, amb la formació de bandes d'elevada densitat intercalades amb bandes de baixa densitat, semblants a les que es troben de manera natural en els camps de cereals. Les bandes depenen de la dispersió de llavors per la segadora però no de la densitat de la població de l’any anterior.

14–El model de simulació de la dinàmica espacial no explica l’aparició de nous rodals isolats que sovint es detecta en els camps, degut a que el procés de dispersió és continu en l’espai. Els nostres resultats suggereixen que la variació espacial i temporal dels paràmetres demogràfics, així com la variació de l’eficàcia de les pràctiques de control de males herbes, han de jugar un paper fonamental en l’establiment de distribucions espacials agregades en rodals. L’efecte d’aquesta variació espacial i temporal sobre la dinàmica espacial de les poblacions ha de ser estudiada en detall per comprendre la distribució en rodals que s’observa en condicions naturals.

15– El model de simulació de la dinàmica espacial prediu una expansió ràpida a tot el camp de la infestació de *L. rigidum* en pocs anys, quasi independentment de la gestió que s’hi faci. Això indica que la taxa d’expansió no depèn de la demografia de la població, sinó solament dels mecanismes de dispersió de *L. rigidum*. Només les pràctiques que minimitzen el moviment de llavors, com ara l’establiment del guaret, o aquelles pràctiques que redueixen dràsticament (més del 95%) la quantitat de llavors que s’incorporen al banc de llavors poden endarrerir l’expansió. L’única manera efectiva de restringir l’expansió dels rodals de *L. rigidum* és el disseny de pràctiques que disminueixin la distància de dispersió alhora que redueixin la quantitat disponible de llavors.

CHAPTER I

GENERAL INTRODUCTION

1. Introduction

1.1. Motivation

Weeds are an important element in cropping systems because they can reduce crop yield and if no action is taken they will reproduce and threaten future crops. Nowadays most cropping systems mainly rely on the use of herbicides, which are generally reliable and relatively cheap. Investment on herbicides has increased constantly since their appearance; from 1960 to 1990 the relative percentage of herbicide sales over those of other pesticides (i.e. mainly fungicides and insecticides, see Table 1) rose from 20% to 45%, and by 1990 world investment in herbicides was about 12600 billion US dollars (Zimdahl, 1999). However, the increasing use (and over-use) of these products has led to greater environmental side-effects. In addition, the public is concerned about herbicide use, particularly issues regarding food safety, water quality, and safety for those handling herbicides and also their effects on the ecosystem. Therefore, new agricultural management practices should aim to reduce herbicides in order to lower their environmental impact and minimise crop yield loss.

Table 1 World sales of crop protection products, 1960 to 1990, with 2000 estimated in billions of dollars (Hopkins, 1994)

Pesticide	**1960**	**1970**	**1980**	**1990**	**2000**
Herbicides	160	918	4,756	12,600	16,560
Insecticides	288	945	3,944	7,840	9,360
Fungicides	320	702	2,204	5,600	7,560
Other	32	135	696	1,960	2,520
TOTAL	800	2,700	11,600	28,000	36,000

Precision agriculture, which advocates the reduction of agricultural inputs (e.g. herbicides) is gaining increasing attention. According to Pierce and Nowak (1999) "*precision agriculture is the application of technologies and principles to manage spatial and temporal variability associated with all aspects of agricultural production for improving production and environmental quality*". However, successful precision agriculture depends on the accurate assessment of variability, and its evaluation and management in space and time. The potential for economic, environmental and social benefits of precision agriculture are largely unrealised because the space-time continuum of crop production remains to be addressed adequately.

1.2. The benefits of managing within field spatio-temporal variability

Cropping systems do not have homogeneous properties across space nor do they behave the same way every year. Weed presence within fields is not an exception. Weed scientists are particularly interested in the weed patch distribution since this could provide the key to making herbicide use more rational and environmentally safe. Many researchers have hypothesised about the benefits of applying the herbicides only on weed patches (Heisel *et al.*, 1997; Lutman & Rew, 1997; Paice & Day, 1997; Christensen & Heisel, 1998; Gerhards *et al.*, 2002; Jurado Expósito *et al.*, 2003) or adjusting the active ingredient and dose of these products in accordance to weed species and density (Forcella *et al.*, 1993; Dieleman *et al.*, 1999; Faechner *et al.*, 2002; Gerhards *et al.*, 2002). These practices constitute site-specific weed management. In other cases, measures may focus on those areas that surpass a certain level of weed pressure, mainly a threshold density (Cousens, 1987; Coble & Mortensen, 1992; Wallinga, 1998; Swanton *et al.*, 1999) that defines (in conjunction with crop value) the amount of area to be sprayed.

However, these management practices imply the extra costs surveying, modelling and managing variability with precision. Clearly, the management of variability should not surpass the potential gain from these practices (Forcella, 1993).

The cost-benefit balance of site-specific management has been studied for several cropping systems (Paice & Day, 1997; Paice *et al.*, 1998; Barroso, 2004). In general, the smaller area infested by weeds and the lower the number of patches, the greater the benefit. However, there are also other constraints to the use of site-specific weed control. In this regard, these authors have also pointed out that the long-term output from these practices can be affected by seed dispersal and the temporal stability of weed patches. In more general terms, as stated by Pierce and Nowak (1999) it is easier to manage parameters with high spatial dependence and low temporal variance than *vice versa*. Therefore, the conditions required for feasible site-specific weed management depend on spatial variability and stability of the management parameters across years.

1.3. Assessing variability

Several studies have analysed spatial variability and modelled the spatial dependence of weed populations (Wiles *et al.*, 1992; Mortensen *et al.*, 1993; Cardina *et al.*, 1995; Cardina *et al.*, 1997; Dieleman & Mortensen, 1999; González-Andújar *et al.*, 2001a; Rew & Cousens, 2001; Faechner & Deutsch, 2002; Wiles & Schweizer, 2002; Jurado Expósito *et al.*, 2003) as a first step for the implementation of site-specific management. Spatial variability modelling has been used mainly draw up detailed maps from data obtained from coarse sampling. Researchers have applied geostatistical techniques (mainly analysis of semivariance and kriging, which are now the most widely used) to describe weed variability. They have also applied geostatistics to redesign sampling methodologies in order to (theoretically) reduce and optimise sampling effort (Wiles & Schweizer, 2002), and to assess the uncertainty in the decision making process (Wiles *et al.*, 1993; Faechner *et al.*, 2002).

Weeds, in spite of the continuous application of herbicides, remain present in crops. However, the main concern of Weed Science is not so much the temporal persistence of weeds but the temporal consistency of patches. Analysis of weed patches from previous years allows to map them once and then treat during the following seasons (Wilson & Brain, 1991; Gerhards *et al.*, 1997b; Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a; Barroso *et al.*, 2004) expecting them not to escape from the mapped area.

Furthermore, spatial analysis offers further advantages. The spatial component of data has been seen in ecology both as a trouble to analyses and as a way to increase the variability explained by models (Legendre & Fortin, 1989; Legendre, 1993). It allows the interpretation of spatial patterns of organisms, of the environmental factors with which they interact and of the joint spatial dependence between organisms and their environment (Rossi *et al.*, 1992). Therefore, researchers should now focus their efforts on elucidating the biological and ecological traits of weeds that lead to patchy distribution and patch stability (or temporal consistency). These data could help to establish the feasibility of site-specific weed management.

1.4. Modelling spatio-temporal variability

In terms of biology and ecology, it is paramount to understand the spatial dynamics of weed patches (Cardina *et al.*, 1997). Moreover, a precise description of weed distribution within fields is crucial for management purposes and to produce realistic models (Rew & Cousens, 2001). It has been postulated that seed dispersal (Rew *et al.*, 1996b; Colbach & Sache, 2001), farm management (Cardina *et al.*, 1997; Dieleman & Mortensen, 1999; Marshall & Brain, 1999; Colbach *et al.*, 2000b), interaction with the physical environment (Andreasen & Streibig, 1991; Häusler & Nordmeyer, 1995; Heisel *et al.*, 1999) and interaction between species (Johnson & Mullinix, 1995) are factors that affect weed dynamics and contribute to patchiness.

An analysis of spatial variability and its evolution using appropriate statistical tools at suitable scale of resolution should provide valuable information on the factors that contribute to determining weed distribution. Several studies have addressed the effect of sampling scale (and design) on the description of spatial variability of weed populations (Rew & Cousens, 2001; Cousens *et al.*, 2002). To understand the spatial population dynamics, the sampling resolution must be appropriate to the mechanisms involved and the specific objectives to be achieved (Rew & Cousens, 2001). If patches coincide with variation in edaphic variables over dozens of meters, the appropriate sampling interval should be more or less the same scale. However, conversely, only mechanisms that act at that scale or greater are detected. If the pattern is to be determined by phenomena acting at metric (or submetric) scale, then much closer sampling distances are required.

However, the temporal stability of spatial distributions should not be overlooked. Most spatial studies consider only the distribution of weeds at a single time point (cf. Rew & Cousens, 2001), but few assess the spatio-temporal stability of patches (Chancellor, 1985; McCanny *et al.*, 1988; Wilson & Brain, 1991; Johnson *et al.*, 1996; Walter, 1996; Gerhards *et al.*, 1997b; Colbach *et al.*, 2000a; Barroso *et al.*, 2004). The displacement of some species is small, whereas others show sudden range expansions, fluctuations at patch margins, colonisation of previously non-infested fields, etc. These observations indicate that a detailed study for each species is required elucidate the dynamics of weed patches. Information on these dynamics and the effects of management practices would allow us to predict the stability or expansion of weed populations.

1.5. The analysis of weed communities

Until now we have referred to “weed” as a general term. However, weeds tend to form mixed communities, whose composition depends on climate, soil characteristics, and crop and tillage history. Weed communities consist of a number of species that differ in life-history traits (i.e. competitiveness, dispersal mechanisms) and interact in complex ways. The outcome of interactions may lead to patchy distribution. Thus, the analysis of the distribution of all weeds in a community can provide a realistic insight into spatial and temporal patterns. The results from these studies could also be extrapolated to similar but unstudied species.

In addition to interactions within and between weed species, weeds also compete with the crop, which is (supposedly) genetically homogeneous and is (supposedly) seeded in an almost regular pattern throughout the field. However, crop yield is not homogeneous across the field, and neither is the output from competition between crop and weeds. Many precision farming scenarios are based on the assumption of stable yield pattern within a field (Colvin *et al.*, 1997). Yield may be highly dependent on many environmental factors, such as soil water holding capacity, soil texture or structure, nutrients, etc. (Earl *et al.*, 2003; Taylor *et al.*, 2003). Furthermore, crop yield can vary over years, depending on the weather, the time of seeding, the time of fertilisation, etc. (Joernsgaard & Halmoe, 2003); consequently also the output from competition with weeds can vary over years.

Those interested in establishing precision farming practices should therefore study the level of spatial and temporal variability of the competitive relationships between the crop and the weed community. The stability of these relationships is the complement to yield stability for the establishment of successful precision farming practices. When weed density–crop yield relationships are not stable within a field, all efforts to produce models will be ineffective.

1.6. The role of seed dispersal on spatio-temporal variability

Some life-history traits of weeds may explain the persistence of patches across years. On the one hand, this stability is enhanced by a persistent seed bank (Mortensen & Dieleman, 1997, 1998; Dieleman & Mortensen, 1999) and pre-harvest seed shedding with no special mechanism for long distance dispersal (Barroso *et al.*, 2004). On the other hand, a transient seed bank and the capacity to disperse long distances can lead to patch instability, the rapid generation of new patches (McCanny *et al.*, 1988; Zhang & Hamill, 1998) and the expansion of those already established (Ballaré *et al.*, 1987b; McCanny & Cavers, 1988; Ghersa *et al.*, 1993).

If seed dispersal processes have a notable effect on the spatio-temporal distribution of a given weed, then the contribution of secondary dispersal by agricultural implements should be determined. Weeds are embedded in a "crop matrix" (here the crop matrix might be understood as the field itself, not the vegetal component only), which is affected by many agronomic operations, like ploughing, seed bed preparation, herbicide application and harvesting. Combine harvesting promotes the rapid spread of weeds (McCanny & Cavers, 1988), thereby causing patches to extend within (Ballaré *et al.*, 1987b; McCanny & Cavers, 1988; Howard *et al.*, 1991) and between fields (McCanny *et al.*, 1988). However, the spatial variability of weed populations have rarely been related to combines (Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a).

1.7. The use of simulation models

The evaluation of the effect of field management on intrinsic populations dynamics, taking into account both the space and time components, may lead to a better understanding of the long-term population dynamics of weeds in fields and to improved weed control. However, this evaluation usually requires vast amount of data on herbicide efficacy, weed–crop interference and weed population dynamics, which, in most cases, are not available. Moreover, the acquisition of these data is difficult, it is almost impossible to set up field experiments for an evaluation of this nature. A widespread alternative to the long-term experimentation is to use models of population dynamics to evaluate the output from weed control programmes (Firbank & Watkinson, 1986, 1987; Cousens & Moss, 1990; González-Andújar & Fernández-Quintanilla, 1991; González-Andújar & Fernández-Quintanilla, 2004). These models also simulate the spatial dynamics of particular weed species (Ballaré *et al.*, 1987a; Perry & González-Andújar, 1993; Wallinga, 1995). Models offer a synthetic insight into the likely output of long-term population dynamics without costly field experimentation and without the uncontrolled variability that field trials intrinsically imply.

The use of mathematical models in spatial population dynamics is a powerful tool for the description, analysis and prediction of the evolution of weed populations (Pacala & Silander, 1990; González-Andújar & Perry, 1995), and they also allow for assessment of the effects of changes in demographic parameters on the model results. This implies that the life cycle stages or management practices that have a stronger effect on the global output can be identified.

2. The species choice

This Thesis focuses on two weed species that are very common in dryland cereal crops. We chose *Avena sterilis* L.[1] and *Lolium rigidum* Gaudin, both annual grass weeds that grow in cereal and other non-irrigated crops, and in disturbed (ruderal) habitats (Bolòs & Vigo, 2001). Although these two plants are native to the Mediterranean basin, they have become important weeds in many other regions with a Mediterranean climate (Martin, 1996). Both weeds are particularly problematic for cereal crops (whether

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[1] *A. sterilis* comprises two subspecies in the North East of Spain (*A. sterilis* L. ssp. *ludoviciana* (Durieu) Gillet et Magne –not ssp. *ludoviciana* (Durieu) Nyman– and the typical subspecies *A. sterilis* L. ssp. *sterilis*) the distribution of which in this territory is not well understood. It seems that the subspecies present in most part of the cereal fields of the Iberian Peninsula is *A. sterilis* ssp. *ludoviciana*. However, it seems to be rare in the North East where there are specimens belonging to *A. sterilis* ssp. *sterilis* that penetrate into the cereal fields. Further studies are needed with regards to the actual distribution of both subspecies. In order to avoid confusing or erroneous use of one name or another, we've decided to keep throughout the Thesis the use of *A. sterilis* whether it is one subspecies or the other.

barley or wheat), and many attempts have been made to characterise the competitive ability against wheat, but always separately for *L. rigidum* (Forcella, 1984; Dowling & Wong, 1993; Lemerle *et al.*, 1995; Lemerle *et al.*, 1996; Taberner, 1996; Cousens & Mokhtari, 1998; Lemerle *et al.*, 2001; Izquierdo *et al.*, 2003) and *A. sterilis* (Martin *et al.*, 1987; Balyan *et al.*, 1991; Torner *et al.*, 1991; González-Andújar & Fernández-Quintanilla, 1993; Dhima *et al.*, 2000; Dhima & Eleftherohorinos, 2001; González Ponce & Santin, 2001). The spatial structure of the populations of these two weeds has been not studied in depth, and only a few authors have included them in more general studies of spatial structure (González-Andújar & Navarrete, 1995; Lamb *et al.*, 1999; Shirtliffe *et al.*, 2002; Barroso *et al.*, 2004). Dispersal behaviour has been reported for *A. sterilis* and very similar species (González-Andújar & Perry, 1995; Shirtliffe *et al.*, 2002), but not for *L. rigidum*. Therefore, the dispersal behaviour of the former was not analysed here and the population evolution simulations under distinct management practices were performed for *L. rigidum* only.

2.1. A brief description of the study species

L. rigidum Gaudin is an annual grass weed belonging to the Pooideae (Festucoideae) subfamily (Dahlgren *et al.*, 1985), tribe Poeae (Tutin *et al.*, 1964). Plants are highly variable in size and appearance, and are generally tufted. The culms (tillers) range from 30 to 80 cm (sometimes more), and are erect or geniculate at the base. The leaves are linear, with the blade 4 to 15 cm × 0.8 cm, with narrow, acute auricles, which slightly embrace the culms. The sheaths of basal leaves are usually purplish pigmented. The prefoliation of seedlings is conduplicated. Leaves and stems are glabrous and lucent. Many culms per plant produce inflorescences. The inflorescence is a slender spike, 8 to 30 cm long, composed of up to 20 spikelets, disposed distichously. The main axis of the inflorescence is very scabrous. The spikelets measure 5 to 18 mm long, and are sessile. Spikelets posses only the lower glume (except the terminal spikelet that has both) which is 7 to 20 mm long, and this does not usually cover all flowers. Each spikelet presents 2 to 10 florets, whose lemmas are from 4 to 10 mm long and present 3 to 5 marked nerves. Lemmas are rarely awned. Once mature, spikelets and seeds disarticulate above the glumes and between the florets, although disarticulation rarely occurs before crop harvest, and seeds disperse in spikelets or whole spike fragments.

At dispersal, the majority of *L. rigidum* seeds are dormant and require a period of dry after-ripening to release dormancy (Steadman *et al.*, 2003a). *L. rigidum* seeds germinate in cereal fields during autumn and winter, although a single hydration–dehydration cycle during summer can considerably accelerate the germination rate (Lush & Groves, 1981; Steadman, 2004); thus, a large fraction of *L. rigidum* seedlings can be already established well in advance of crop emergence. Ungerminated seeds have a relatively short life in the seed bank (Gill, 1996a). Vegetative development and flowering take place in spring. Seedlings begin to produce tillers at the end of winter –growth stage 2 of the decimal scale of Zadoks *et al.* (1974)– and by the end of the tillering they develop much faster (Taberner, 1996). *L. rigidum* shows a high fecundity. Seed production can attain 900 to 1000 seeds per plant (Recasens *et al.*, 1997) although seed production might be highly dependent on intra and interspecific competition, and also on weather conditions during development (Fernández-Quintanilla *et al.*, 2000; Izquierdo *et al.*, 2003).

L. rigidum inhabits mainly wastelands, roadsides and annual crops, but it also appears in therophytic pastures and chamaephytic pastures in Mediterranean habitats, between 0 and about 1450 m above sea level. It is one of the most widespread weeds in Spanish drylands, especially in the North-East. According to several surveys, *L. rigidum* is present in more than 50% of the cereal fields of Catalonia (Recasens *et al.*, 1996) where it has become the dominant (and sometimes the only) weed because of the change in the agronomy of the cereal crops (increasing herbicide pressure, direct seeding). *L. rigidum* can be an extremely competitive weed in cereal crops (Lemerle *et al.*, 1996; Cousens & Mokhtari, 1998; Lemerle *et al.*, 2001). Its invasive success is enhanced because of its high genetic variability (Gill *et al.*, 1996), seed production (Monaghan, 1980; Gill, 1996a, b) and seed survival over summer and autumn (Gramshaw & Stern, 1977). Moreover, in recent years many herbicide-resistant genotypes have been detected (Matthews, 1996a). Since 1982, resistance to up to 10 herbicide action groups has been reported (Llewellyn & Powles, 2001; Llewellyn *et al.*, 2002). Specifically, ACCase inhibitor resistance in *L. rigidum* threatens cereal production in Australia, Canada, Chile, France, South Africa, Spain, the United Kingdom and the USA (Heap, 1997).

A. sterilis L. is an annual grass weed that belongs to the Pooideae (Festucoideae) subfamily (Dahlgren *et al.*, 1985), tribe Aveneae (Tutin *et al.*, 1964). Plants are erect or geniculate, caespitose. Culms are 55-160 cm high, and are not branched above. Leaves are mostly basal and basal leaf sheaths can be glabrous or pubescent to pilose. Leaf blades measure up to 60 cm × 1.4 cm. The leaves do not have auricles but present a ligule 2.5-8 mm long, almost triangular in shape, decurrent, membranous, obtuse, entire or truncate. Leaf blades join the sheath gradually, have a prominent midrib and scabrous or ciliate margins. Prefoliation is convolute. The inflorescence is a panicle, pallid and green, nodding, open, symmetrical or nearly symmetrical, and fully exserted. The main inflorescence axis measures up to 45 cm × 25 cm. The primary inflorescence branches are scabrous; paired or clustered, sometimes branching at the base, and carry 1 or 2 pendulous spikelets. Spikelets are 20 to 45 mm long. They are laterally compressed, and are formed of 2 to 5 florets. Only the lowest 2 florets are awned; the awns are black coloured, bent, twisted and dorsal, and measure up to 8 cm. The florets distal to the hermaphrodite ones are rudimentary. The spikelets do not disarticulate as a separate unit, but they do above the glumes (between the upper glume and lowest lemma only). The lemmae are firmer than the glumes; they present a hairy (bristly) abaxial surface and are bifid at the apex (lobes occasionally with a short bristle). Seeds disperse readily when mature, usually before crop harvest under Spanish conditions.

A high proportion of the seed population is dormant –up to 95%– with a relatively long life –up to 43 months– (Sanchez del Arco *et al.*, 1995). Seeds present at least two sources of dormancy (endogenous and exogenous) that are gradually released, as a response to temperature and soil moisture (Fernández-Quintanilla *et al.*, 1990). *A. sterilis* responds to cooler temperatures compared to other *Avena* species (Fernández-Quintanilla *et al.*, 1990; Medd, 1996a) and germination occurs in autumn, winter and early spring. Although the development of this weed is fairly parallel to that of the cereal in spring is usually faster. Mature individuals produce and shed seeds before crop harvest. Seed production per plant is usually low –12 to 30 seeds per panicle or up to 50 seeds per plant– (Sanchez del Arco *et al.*, 1995; Medd, 1996a), although seed production from untreated plants can reach up to 10000 seeds m^{-2} (Medd, 1996a).

A. sterilis inhabits mainly wastelands, roadsides and annual crops between 0 and 1400 m above sea level. It is the more abundant and extended weed in cereal crops in Central Spain and in many other regions with Mediterranean climate. *A. sterilis* is a highly competitive plant and reduces crop yields and, to a much lesser extent, crop quality (Medd, 1996b). *A. sterilis*, like other *Avena* species, is among the most competitive weeds in wheat (Poole & Gill, 1987; Torner *et al.*, 1991; González Ponce & Santin, 2001). In addition, multiple resistance to several herbicide action groups has been detected (Nietschke & Medd, 1996; Heap, 1997; Cavan *et al.*, 1998).

3. Objectives

This Thesis evaluates the distinct "spatial" topics of the biology and ecology of *A. sterilis* and *L. rigidum* in cereal fields, in order to elucidate the effects of dispersal and competition with *A. sterilis* on the spatial structure and dynamics of *L. rigidum* in cereal fields, which can have a profound effect on the output from site-specific management. This study aims to:

a) Compare the spatial pattern of *Avena sterilis* and *Lolium rigidum* within a single field at contrasting spatial scales in order to detect the factors that drive the evolution of the spatial structure of the assembly of these two species (Chapter II).

b) Assess the short scale spatial and inter-annual stability of the competitive capacity of *A. sterilis* and *L. rigidum* in mixed communities against wheat in terms of yield reductions, using synchronic and diachronic studies at contrasting topographical positions (Chapter III).

c) Analyse the effect of different kinds of combines on the seed dispersal of *L. rigidum* and evaluate the relationship between secondary seed dispersal by this farm machinery and the fine-scale spatial distribution of seedlings (Chapter IV).

d) Evaluate the effect of spatial population dynamics of *L. rigidum* with respect to the predictions of non-spatial population models and study the evolution of weed patches within a previously uninfested field in relation to weed management practices (Chapter V).

4. The study sites and the experimental approach

To fulfil these objectives, we performed several experiments at two sites, one to address the spatio-temporal evolution and the other for dispersal by combines.

Dispersal by combines was studied in a small field (1.8 ha) in Concabella (La Segarra, Catalonia, 41º40’51” North 1º20’6” East). The field was selected because it had no natural infestation of *L. rigidum*, and allowed for the design of the different plots and replicates required within a single flat and homogenous surface. Although the positioning of the different plots and replicates ensured harvesting with a minimum of combines passes, the field was large enough to avoid overlap between plots and replicates during seed dispersal.

Spatio-temporal studies of competition and structure in a mixed weed community were performed in a medium sized field (8 ha) located in Calonge de Segarra (L’Anoia, Catalonia, 1º31’29” E 41º45’32” N,). Field choice was based on several criteria. The field had to be a large enough field to allow for some intra-field variability in soil parameters or at least have an irregular topography, in which distinct areas could be distinguished by exposure and slope. The field also had to have irregular infestations of *L. rigidum* and *A. sterilis* and have been sown with small grain (cereal) in recent years. Using these selection criteria, a field was selected from a previous cereal field survey.

Only a 1.90 ha rectangular area (150 m × 130 m) was used in the experiments. This part of the field was topographically irregular with differences in elevation of up to 10 m, although it was within a single drainage system, running from the south-eastern corner to the north-western corner. The north eastern corner (the top most part of the field) was a south facing back slope with a steep section. The soil texture of the whole field ranged from loam to clay loam, and differences between zones were negligible. The topographical and soil heterogeneity was expected to influence weed infestation and the competitive relationships between crop and weeds.

Weed community was dominated by *L. rigidum*, and, in some well defines zones *A. sterilis* was also present in abundance. Another annual weed species, such as

Polygonum aviculare L., *Papaver rhoeas* L., *Polygonum convolvulus* L., *Chenopodium vulvaria* L. and *Kickxia spuria* (L.) Dumort (in order of decreasing abundance), were also present. Only some individuals of perennial weeds, such as *Euphorbia serrata* L., *Centaurea scabiosa* L. and *Gagea villosa* (Bieb.) Duby were present. The *A. sterilis–L. rigidum* assembly was chosen for a more thorough analysis since it is one of the most characteristic and consistent weed assemblies in winter wheat and winter barley fields not only in Spain but also in many areas with a Mediterranean-like climate. Dicotyledonous weeds are a really minor component of the weed community in many conventionally managed cereal fields (at least in north eastern Spain), and hardly never have a leading role in weed community (except *Cirsium arvense* (L.) Scop. in some cases).

The weed community was selectively managed during the study. Given our interest in the intrinsic demographic patterns of the dominant weeds (specially *L. rigidum*) and in the effects of weeds on crop yield, although grass weeds were dominant *per se*, graminicides were avoided at the beginning of the experiments; however, broad-leaf herbicides were scheduled yearly. To prevent a massive build up of grass weed populations, diclofop-methyl was used at half the recommended rate in the second year.

This study focused on a two-species community and may not reflect field conditions. However, this design was selected in order to overcome the limitations of single species studies. Moreover, single-weed studies are usually performed under controlled conditions, with weeds sown at the required densities, and experimental designs free of other weed species. The fieldwork proves to be a source of problems (in design, management and statistical treatment of data) but also an invaluable source of information on the real (temporal and spatial) variability of biological processes. Weed-community field studies could offer a more comprehensive vision of the true dimensions of the problem caused by these plants.

CHAPTER II

SPATIAL AND TEMPORAL PATTERNS OF *LOLIUM RIGIDUM–AVENA STERILIS* ASSEMBLIES IN CEREAL FIELDS

Summary

Through a detailed case study of a two-species (*L. rigidum* and *A. sterilis*) weed community at contrasting scales, this paper aims to throw some light on the various factors that affect weed distribution across space and time. *A. sterilis* showed fairly stable spatial distribution and spatial structure of its population across time at large scale, with well-defined patches, although weed population can rise quickly, which may cause some statistical methods to miss spatial stability. *L. rigidum* showed poorly defined patches (though a clear trend in one direction) that were not stable across time. Interaction between species could also explain to some degree spatial distribution at large scale. At fine scale both species showed a clear interaction effect from primary dispersal (more important in *A. sterilis*) and secondary dispersal from combine harvesting (more important in *L. rigidum*).

1. Introduction

The spatial distribution of weeds within fields has received increased attention in recent years. In theoretical terms, it is crucial to understand the spatial dynamics of weed patches in order to achieve realistic models of weed populations (Cardina *et al.*, 1997). Further, accurate description of weed distribution within fields is crucial for weed management (Rew & Cousens, 2001). Seed dispersal, farmer management, interaction with the physical milieu and interaction with other species are all factors that affect weed dynamics and contribute in one way or another to weed patchiness.

The description of weed spatial variability at different scales can give us insight into all these factors, the way they interact and their relative importance in the spatial distribution of weeds. However, the effect of the sampling scale should not be overlooked. Description of spatial variability of weed populations at different scales has been reviewed by some authors (Rew & Cousens, 2001; Cousens *et al.*, 2002). Different sampling designs for investigating the factors leading to actual distribution of weeds at different scales have been assayed. Large-scale sampling (i.e. whole-field sampling, regional distribution) was undertaken when the aim was to detect relationships between weed distribution and ecological gradients (Häusler & Nordmeyer, 1995; Heisel *et al.*, 1999; Cousens *et al.*, 2002) and management (Colbach *et al.*, 2000a). With fine-scale sampling (part of a field, intra-patch sampling) researchers described the factors driving seed dispersal, factors causing variation within weed patches and the internal dynamics of patches (Cousens *et al.*, 2002; Shirtliffe *et al.*, 2002; Blanco-Moreno *et al.*, 2004).

Usually, weed communities consist of several species that differ in life-history traits (i.e. dispersal mechanisms, competitiveness) and interact with each other in complex ways. For this reason, joint spatial structure analyses give a realistic perception of spatial and temporal patterns. Thus, the comparison of the spatial variability of different species in a single field and consequently under the same biotic, agricultural and abiotic factors may help identify the mechanisms that lead to patchy distribution and extrapolate to similar but unstudied species. Only a few studies have dealt with such comparisons (Clay *et al.*, 2000; Colbach *et al.*, 2000a), and unfortunately these only focused on large-scale sampling, so missing information on processes working at a finer scale than the whole field.

Lolium rigidum Gaudin (annual ryegrass) and *Avena sterilis* L. (wild oat) are two of the major grass weeds in Mediterranean dryland crops (González-Andújar & Fernández-Quintanilla, 1993; Gill, 1996b; Medd, 1996b; Recasens *et al.*, 1997). Although they have been studied for a long time because of their effects on crop yield (Pannell & Gill, 1994; Lemerle *et al.*, 1995) and the world-wide appearance of resistant genotypes (Heap, 1997), they have been largely disregarded in spatial structure studies. Only some weeds of the genus *Avena* have been the subject of some studies of spatial structure (Lamb *et al.*, 1999; Rew *et al.*, 2001; Shirtliffe *et al.*, 2002), which provided certain guidelines for the site-specific management of such weeds.

In addition, weed communities of winter wheat crops in many Mediterranean-climate areas are usually dominated by *L. rigidum* and *Avena* sppl. assemblies (Pannell & Gill, 1994), with few broad-leaved weeds present in such agro-ecosystems. This adds special interest to the joint description of the spatial structure of both weeds, since it could reflect the real situation in many cereal fields. Moreover, these two weeds might illustrate other biological and agronomic phenomena. *Avena* species are far more competitive than *L. rigidum* (Pannell & Gill, 1994), which can lead to inequalities between them in competition with the crop, which could, for instance, limit seed production. Their dispersal mechanisms also differ: primary dispersal of *L. rigidum* is very limited because most seeds do not spontaneously fall from spikes, but are spread by combine harvesters dozens of meters (Blanco-Moreno *et al.*, 2004). In contrast, *A. sterilis* sheds most seeds before the crop harvest, resulting in minimal dispersal by combines (Barroso *et al.*, 2004). The effect of other agricultural operations such as cultivation on the dispersal of weed seeds is thought to be much less important (Howard *et al.*, 1991; Colbach *et al.*, 2000b; Blanco-Moreno *et al.*, 2004).

The aims of this study were to evaluate the spatial structure of *L. rigidum* and *A. sterilis* populations and their development over three years at large scale and to relate their spatial variability to dispersal mechanisms and interference relationships. The paper also compares the fine-scale spatial patterns of both species and discusses them in relation to dispersal behaviour and management practices.

2. Material and Methods

2.1. Field site

To examine the interference relationships and evolution of the spatial structure of the two species, all sampling was carried out in a cereal field dominated by *L. rigidum* and *A. sterilis*, so avoiding the confusing effect of companion species. Weed species differed in abundance and distribution pattern, which aided the detection of changes over time. To avoid the misleading effects of herbicides on the intrinsic population dynamics of weeds and on the increase of weed patches, the experience was initially designed without grass-weed herbicides (however, see below for detail of herbicide use) because the chemical control is known to reduce weed population sizes and spatial distribution of some species (Barroso *et al.*, 2004).

Field surveys of grass weed populations were conducted from 2001 to 2003 at a commercial field at Calonge de Segarra (Central Catalonia, north-east Spain, 41º45’32” North 1º31’24” East) to analyse the spatial structure of populations of *A. sterilis* and *L. rigidum*. The 8-hectare field was irregularly shaped, and only 1.95 ha of the field were surveyed. The topography was heterogeneous, with differences in height of up to 10 m. The entire surveyed surface belonged to one single drainage system, which run approximately from the south-eastern corner to the north-western corner. The soil texture of the field ranged from loam to clay loam. Preliminary analyses showed there was no clear relationship between weed distribution and soil properties (Sans *et al.*, 2002; Blanco-Moreno *et al.*, 2003): management history before the beginning of the experiment was probably responsible for the spatial distribution of weeds.

Each year in late October the field was sown with *Triticum aestivum* L. cv. Soissons at 180 kg ha^{-1} with the farmer’s own seeding equipment. All agricultural operations (sowing, harvesting and ploughing) were done approximately in the East to West direction, following minimum slope lines. Fertiliser was added twice; a granular application of NPK 10-15-15 at 325 kg ha^{-1} before sowing and a liquid application of SN32 (Urea-Nitrate-Ammonium) at a rate of 280 kg ha^{-1} in the winter. Weeds were controlled with post-emergence herbicides. Broad-leaf weeds were treated with a mixture of herbicides (chlorsulfuron at 9 g.a.i. ha^{-1} plus tribenuron-methyl at 9.375 g.a.i.

ha^{-1}) every year. In 2001 there was no treatment for grass weeds to allow monitoring of the intrinsic dynamics of target species, but in 2002 there was an application of diclofop-methyl at 350 g.a.i. ha^{-1} to prevent a large increase in weed populations. However, there is some evidence that at least the *L. rigidum* population has some degree of resistance to diclofop-methyl and to tralkoxidym (J. Recasens & A. Taberner, pers. comm.). Moreover, heavy rainfall after herbicide application led to wash-off and reduction of herbicide effect.

Weed individuals were identified and counted prior to post-emergence applications (from January 7 to 30, depending on year). Weed density by species was obtained at the same locations each year.

2.2. Sampling

2.2.1. Large-scale sampling

In order to ensure regular sampling, a 16-column × 14-row grid (150 m wide East–West × 130 m long North–South) was established approximately in the middle of the field. Distances between grid points were 10 m in both north-south and east-west directions. Sampling plots were georeferenced using a sub-metre accuracy Ashtech G-12 (Magellan Corporation, Santa Clara, California, USA) differential global positioning system (DGPS) to ensure accurate re-location each year.

Densities of both weeds were evaluated in all grid nodes. Because of the high weed density and the sub-metric spatial variability of populations, *L. rigidum* density was evaluated in nine 10 cm × 10 cm quadrats, randomly placed within a 1 m × 1 m area to increase support for density observations. *A. sterilis* density was evaluated in different ways. *A. sterilis* density in 2001 and in 2002 was evaluated at harvest in four 25 cm × 25 cm quadrats randomly placed within each area. Previous studies had found that *A. sterilis* density was rather constant from seedlings to mature plants: seedling survival is high (>70%) at low to medium densities (up to 200 seedlings m^{-2}) (González-Andújar & Fernández-Quintanilla, 1991; González-Andújar & Fernández-Quintanilla, 1993; González-Andújar, 1997). *A. sterilis* density in 2003 was estimated with the same system as for *L. rigidum*.

2.2.2. Fine-scale sampling

Four 10 m × 10 m areas were selected in 2002 for the study of fine-scale structure of both weed populations. The areas were selected to cover a range of weed densities. However, *L. rigidum* density was high and fairly homogeneous throughout the field, so differences in density between areas were unimportant. The density of *A. sterilis*, which was much more localised in the field, varied greatly between the surveyed areas. These 10 m × 10 m areas were sampled in a 21 column × 21 row grid; there were 441 nodes 0.5 m apart. In each node, *L. rigidum* and *A. sterilis* densities were recorded in a 10 cm × 10 cm quadrat.

2.3. Data analysis

2.3.1. Large and fine-scale spatial distribution

Summary statistics (mean, median, minimum and maximum, skewness, kurtosis and percentage of records with zeros) were computed for each weed species. Because seedling counts were positively skewed (only slightly for *L. rigidum* in 2003, Table 1), in all cases $\log_{10}(z+1)$ transformation was used in subsequent analyses. Transformation is also useful to avoid non-normality and heteroscedasticity in data. Independence of means and variances was examined according to Hamlett *et al*. (1986).

Table 1 Statistical description of *Lolium rigidum* and *Avena sterilis* infestations in the study field for all three years.

Variable	Mean	Median	Minimum	Maximum	Variance	Kurtosis	Skewness	% Zeros
A. sterilis								
2001	12.34	0.00	0.00	152.00	590.02	9.09	2.85	54.02
2002	44.93	12.91	0.00	319.96	4813.21	3.52	2.03	24.11
2003	225.25	105.56	0.00	1066.67	71854.28	0.96	1.40	12.95
L. rigidum								
2001	454.27	311.11	11.11	2688.89	177013.22	5.44	1.98	0
2002	1709.37	1533.33	222.22	5077.78	815013.86	1.10	0.96	0
2003	2225.25	2133.33	388.89	5288.89	821081.98	-0.20	0.41	0

Spatial trends in weed density data were removed by means of the median polish algorithm (Cressie, 1993; Cardina *et al.*, 1995), which, in a grid, breaks down the values into a row effect, a column effect and the residual that is used in the geostatistical analysis:

$$z'_{ij} = z_{ij} - \tilde{z}_{\cdot j} - \tilde{z}_{i\cdot} + \tilde{z}_{\cdot\cdot} \tag{1}$$

where z'_{ij} is the median polish residue for point *ij*, $\tilde{z}_{ij}$ is the log-transformed data value, $\tilde{z}_{\cdot j}$ is the j^{th} row log-transformed median, $\tilde{z}_{i\cdot}$ is the i^{th} column log-transformed median and $\tilde{z}_{\cdot\cdot}$ is the global log-transformed median. The results from the log-transformed data (which will be referred herein as to raw data) were compared with the median polish residues (referred to as detrended data), to assess the effect of trends on geostatistical assumptions.

Within each year, spatial dependence between samples was analysed with the correlogram expressed in terms of a semivariogram. The correlation index has been described in depth elsewhere (Isaaks & Srivastava, 1989; Rossi *et al.*, 1992; Deutsch & Journel, 1998); its advantage over other measures of spatial continuity is that it offers a standardised measure of spatial dependence which is useful when comparing variables with disparate levels of variability (Rossi *et al.*, 1992). In addition, a correlogram provides a better interpretation of spatial pattern than a semivariogram when local means and variances change within the domain. Moreover, spatial correlation can be modelled even in the presence of trend in the data, since the effects of varying local means and variances are filtered (Rossi *et al.*, 1992; Wiles & Schweizer, 2002). To keep consistency with geostatistical tradition, all correlograms are here expressed in terms of standardised semivariance, according to the relationship:

$$1 - \rho_h = \gamma_h / \sigma^2 \tag{2}$$

where ρ_h is the correlation coefficient at distance h, γ_h is the semivariance at distance h and σ^2 is the sample variance.

Correlograms were computed in four directions in space (0, 45, 90, 135 degrees clockwise from north) with minimal angular and bandwidth tolerances (11.2 degrees and 20 m), in order to obtain a clear directional correlogram through the use of strictly aligned pairs of points. Small angular and bandwidth tolerances should ensure retaining as much of the original anisotropy as possible (Isaaks & Srivastava, 1989; Deutsch & Journel, 1998), although it reduces the quantity of data pairs included in each of the correlogram points. For a more detailed description of geostatistical methods to summarise spatial structure see any basic geostatistics treatise (Clark, 1979; Isaaks & Srivastava, 1989; Legendre & Fortin, 1989; Deutsch & Journel, 1998) and, more specifically to weed science, see a recent study dealing in detail with terminology and procedures (Wiles & Schweizer, 2002). Sample correlograms were calculated by means of the semivariogram procedure (PROC VARIOGRAM) of SAS (SAS, 1999) and a post-processing of results to convert them into correlogram values. Correlation coefficient can vary between -1 and 1, but standardised semivariance should theoretically be bounded between 0 and 1; so, although the expression 1-ρ_h could yield values greater than one, the maximum allowable semivariance value (the sill) was 1. This makes sense, in that our primary interest is to define the distance at which observations become independent (the range, in geostatistical jargon):

$$\begin{gathered}\rho_{range} = 0 \\ 1 - \rho_{range} = \gamma_{range} / \sigma^2 = 1\end{gathered} \tag{3}$$

where ρ_{range} is the correlation coefficient at the range, γ_{range} is the semivariance at the range and σ^2 is the sample variance. All sample correlograms were modelled with the same functional form so that comparisons between species and years would be straightforward. Two nested spherical models with a nugget effect were used to model the spatial correlation structure of the seedling counts:

$$\gamma(h) = \begin{cases} c_0 & \text{if } h = 0 \\ c_0 + c_1\left(1.5\left(\frac{h}{a_1}\right) - 0.5\left(\frac{h}{a_1}\right)^3\right) + c_2\left(1.5\left(\frac{h}{a_2}\right) - 0.5\left(\frac{h}{a_2}\right)^3\right) & \text{if } 0 < h < a_1 \\ c_0 + c_1 + c_2\left(1.5\left(\frac{h}{a_2}\right) - 0.5\left(\frac{h}{a_2}\right)^3\right) & \text{if } a_1 \le h < a_2 \\ c_0 + c_1 + c_2 & \text{if } h \ge a_2 \end{cases} \tag{4}$$

where c_0 is the nugget effect, c_1 and c_2 are the respective contributions of the first and second spherical model, a_1 and a_2 are the ranges of the spherical models and h is the lag distance.

Correlograms were modelled using the four directional sample correlograms. The variation in all four axes is modelled jointly with an ellipse that is described with the minimum and maximum radii lengths and the direction of the axis in relation to the main directions (north-south and east-west). The range in each direction is then specified through the polar equation of the ellipse, which states that:

$$a_\alpha = \sqrt{\left(a_{max}^2 \cdot a_{min}^2\right) / \left(a_{max}^2 \cdot \sin^2\alpha + a_{min}^2 \cdot \cos^2\alpha\right)} \qquad (5)$$

where a_α is the range in the α direction, a_{max} is the maximum radius of the ellipse model and a_{min} is the minimum radius of the ellipse. A single model of spatial variation is then fitted simultaneously to all directions using the non-linear regression procedure (PROC NLIN) of SAS (SAS, 1999) with weighted least squares (Cressie, 1985). To preserve clarity in subsequent figures, we opted to show only two main directions in semivariograms: 90º from North-South direction, which was approximately the direction of crop rows; and 0º, the perpendicular direction.

2.3.2. Spatial stability of populations and spatio-temporal interspecific relationships

Year-to-year population stability of each target species and relationships between species were analysed only at large scale, because spatial structure of populations at fine scale is (as will be shown) highly dependent on agricultural factors that are not consistent from year to year. Stability of weed populations was measured by the Pearson correlation coefficient with raw and detrended data and also by the codispersion coefficient $\rho_{XY}(h)$, which is defined as:

$$\rho_{XY}(h) = \frac{\gamma_{XY}(h)}{\sqrt{\gamma_{XX}(h)\gamma_{YY}(h)}} \qquad (6)$$

where $\gamma_{XX}(h)$, $\gamma_{YY}(h)$ and $\gamma_{XY}(h)$ are, respectively, the semivariance coefficient of variable X, the semivariance coefficient of variable Y and the cross-semivariance between X and Y at lag distance h. The rescaling of cross semivariance values by the corresponding direct semivariance values yields the codispersion coefficient, which can be interpreted as a linear correlation coefficient between the spatial increments of both attributes (Goovaerts, 1998). Here the X and Y variables are the same weed in different years (e.g. *L. rigidum* in 2001 and *L. rigidum* in 2002). The codispersion coefficient was computed only with detrended data, since results of raw and detrended data were roughly the same and so the inclusion of both added no relevant information.

Spatial stability of weed populations was also measured by means of the statistical test proposed by Syrjala (1996) to test for a difference between the spatial distribution of two populations. The test is a modification of a Cramér–von Mises non-parametric test for a difference between two univariate probability distribution functions. This test has been used recently to analyse the spatial stability of *A. sterilis* population changes over time (Barroso *et al.*, 2004). For statistical considerations, since this is a randomisation test, the test is conducted over 1000 permutations (Syrjala, 1996).

The spatio-temporal interspecific relationships were analysed by means of the Pearson correlation coefficient (with raw and detrended data), which provides a static non-spatial analysis of the relationship of the relative values of both species, and also by means of the codispersion coefficient. In this case, the X and Y variables are the densities of different species in the same or different years. The computation of correlation and codispersion coefficients between species in different years shows the effect of previous populations on actual distribution.

3. Results

3.1. Changes in *L. rigidum* and *A. sterilis* population density

Each species performed differently during the course of the study. Frequency distribution for both weeds showed strong skewness in the first year, as is usual in the literature for most weed counts. In the case of *A. sterilis,* skewness was still more marked because of the high number of plots with zero counts (Table 1). In the case of *L. rigidum,* as a result of increased density, the population became more homogeneous across the field and frequency distribution became nearly symmetrical (Table 1). During the course of the study, both weeds increased their numbers, despite the herbicide treatment in 2002. During the experiment, mean density of *L. rigidum* increased by 489.9%; and of *A. sterilis,* by 1825.4%.

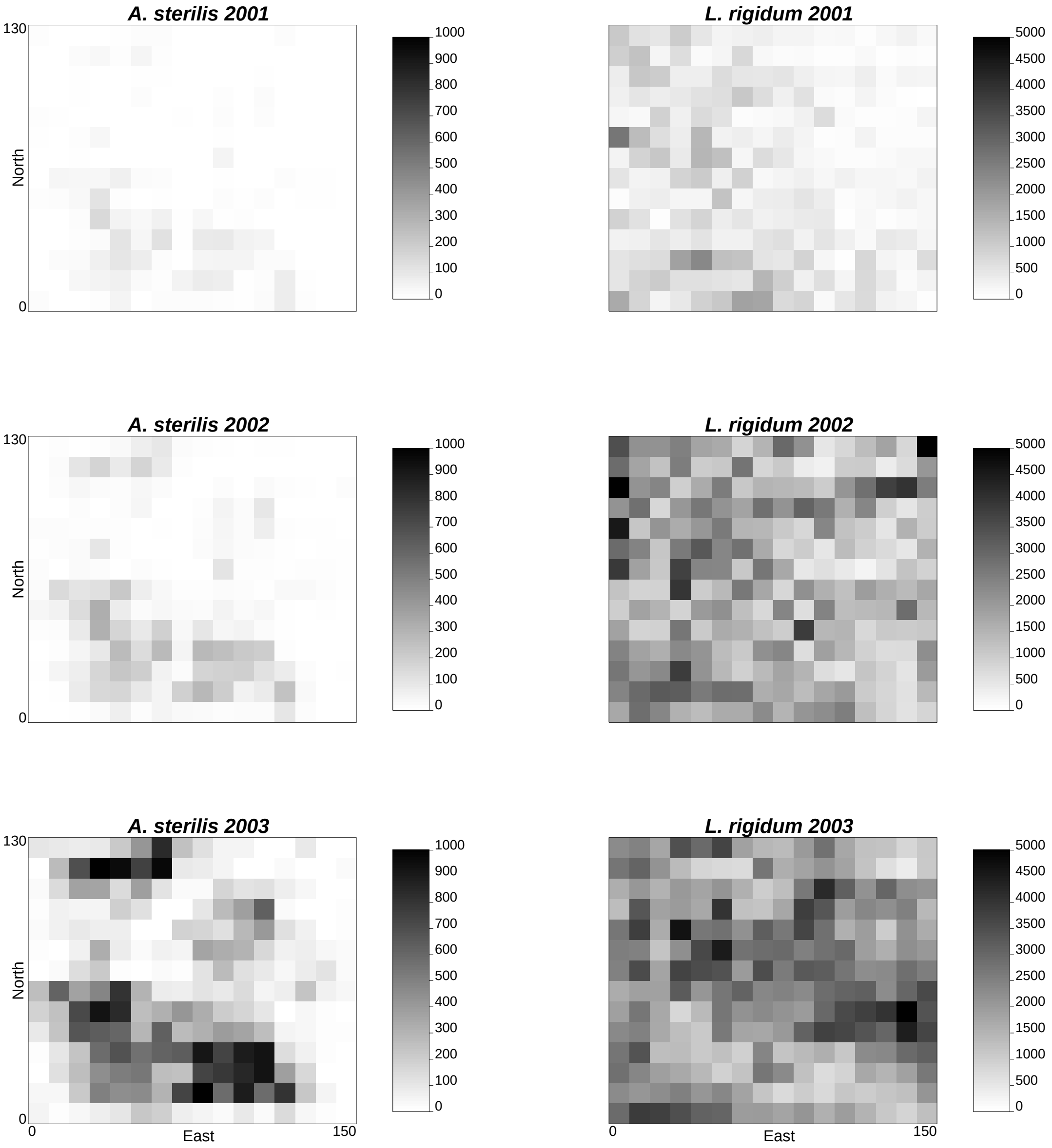

Fig. 1 Density maps at large scale for *Avena sterilis* and *Lolium rigidum* in each of the three years. Note that the scales are independent for each weed species. Crop rows were oriented East to West.

A. sterilis showed marked expansion of patches: 54% of the plots were free of this weed in 2001 but only 24.1% were in 2002, and only 12.9% in 2003 (Table 1 and Fig. 1). Since no plot was free of *L. rigidum*, no expansion of patches was detected, but rather a reorganisation of maxima and minima. *L. rigidum* population increased at 97.7% of the points sampled between 2001 and 2002, while it decreased at 33% of the sampling points between 2002 and 2003. Changes were much larger between 2001 and 2002 than between 2002 and 2003.

3.2. Large-scale spatial distribution of *L. rigidum* and *A. sterilis*

Spatial dependence of populations was detected for both species in all years (Table 2 and Fig. 2). Semivariograms depicted, at least to some extent, spatial correlation of weed populations. Empirical semivariograms performed with raw data of both species surpassed the theoretical sill value 1 in some directions (Fig. 2B-C, 2G-I).

Table 2 Correlogram parameters for both species in each of the three years at large-scale sampling, as estimated by weighted least squares from the log-transformed (raw) data and the median polish (detrended) data.

	c_0	c_1	a_{1max}	a_{1min}	α_1	c_2	a_{2max}	a_{2min}	α_2
Raw data									
A. sterilis									
2001	0.27	0.24	63.37	17.94	0.00	0.49	173.02	64.10	66.18
2002	0.16	0.36	152.94	32.01	-11.40	0.48	137.56	41.97	72.49
2003	0.11	0.23	6347.25	40.45	1.51	0.66	51.21	33.39	97.12
L. rigidum									
2001	0.40	0.14	249.92	2.70	89.29	0.46	321.12	110.02	14.24
2002	0.53	0.29	1251.13	16.05	103.60	0.18	4772.35	93.07	12.49
2003	0.00	0.48	24.38	16.53	127.43	0.52	899.96	29.24	73.29
Detrended data									
A. sterilis									
2001	0.36	0.30	11.58	36.81	86.02	0.34	164.30	34.24	18.79
2002	0.20	0.43	99.10	8.06	84.17	0.37	62.10	53.54	82.75
2003	0.00	0.67	32.41	14.80	56.09	0.33	50.49	28.22	65.87
L. rigidum									
2001	0.60	0.06	10	14.42	99.50	0.34	32.98	6.89	103.02
2002	0.34	0.53	9946.59	8.73	119.28	0.14	3291.93	18.55	110.42
2003	0.03	0.72	34.97	16.88	105.70	0.25	151.20	24.12	55.38

c_0 is the nugget effect; c_1 is the contribution of the first spherical model; a_{1max} is the range in the direction of maximum continuity and a_{1min} is the range in the perpendicular direction of the first spherical model; α_1 is the direction of maximum continuity, in degrees clockwise from North, of the first spherical model; c_2 is the contribution of the second spherical model; a_{2max} is the range in the direction of maximum continuity and a_{2min} is the range in the perpendicular direction of the second spherical model; α_2 is the direction of maximum continuity, in degrees clockwise from North, of the second spherical model.

Hole effects occurred for *A. sterilis* seedling populations. Hole effect was more or less clearly evident all years in *A. sterilis* spatial structure in the 90º direction –parallel to crop rows– and the adjacent directions (45 and 135º, data not shown). Hole effects were not modelled because the distance at which the correlogram first reaches the sill is considered the range of spatial dependence. Moreover, since the processes that create periodicity commonly act in one direction (Isaaks & Srivastava, 1989), determining the distance at which the first bump is present in that direction is sufficient. The *L. rigidum* population displayed no clear hole effect in any direction at large scale.

Although zonal anisotropy was detected in raw data for *L. rigidum* in 2001 and 2002 (Fig. 2G,H) and for *A. sterilis* in 2003 (Fig. 2C), it disappeared from the 0º and 90º directions in the analyses of detrended data (Fig. 2D-F and Fig. 2J-L). For the 0º direction, the semivariogram did not attain the theoretical sill within the study domain (Fig. 2G-H).

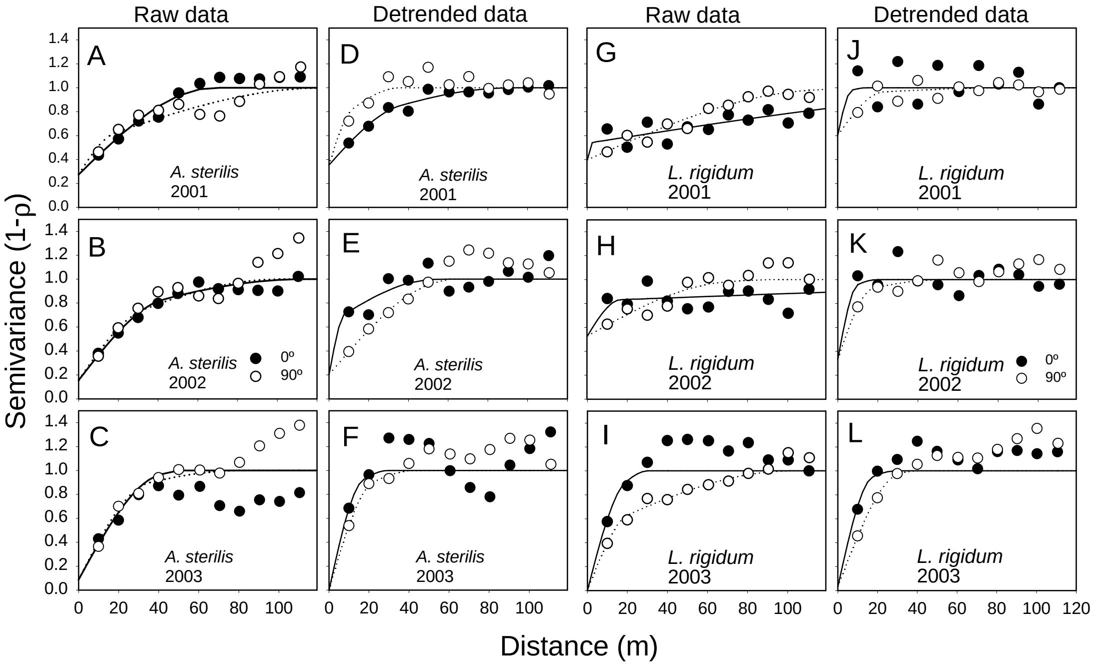

Fig. 2 Spatial structure at large scale of *Avena sterilis* and of *Lolium rigidum*, inferred from log-transformed (raw) and median polish (detrended) data. Symbols indicate the values of the experimental semivariograms and lines show the model fit by weighted least squares. Dots (●) represent the 0º (across crop rows) direction; and circles (○), the 90º (parallel to crop rows) direction.

Two spherical models were commonly needed to describe correctly hole effects and the rapid increase of semivariance at short distances. The contribution of the spatial component (1- c_0) to total variation of populations ranged from 47% to 100% (see Table 2), depending on year and species. Spatial autocorrelation at shorter distances was generally stronger for the *A. sterilis* population; the nugget effect ranged from 11% to 27% of total variation (mean = 18.0%). *L. rigidum* showed weaker spatial structure: the nugget represented 40% of total variation in the first year, whilst it was about 0% in the third year (mean of the three years, 32.3%). Moreover, both species generally showed a decrease in non-structural variability (nugget semivariance) over the three years (Table 2).

Spatial variability usually increased rapidly with distance up to the range of the first spherical structure, and then flattened partially between the first and second structure ranges (especially clear in Fig. 2D, 2E, 2I). However, the relative contribution of both structures (the ratio between c_1 and c_2) and the ranges and direction of maximum continuity were not consistent across years for either species (Table 2).

3.3. Fine-scale spatial distribution of *L. rigidum* and *A. sterilis*

Fine-scale sampling revealed spatial dependence of both weed populations in all plots (Table 3 and Fig. 3). The level of non-structural variation (nugget effect) was under 50% in all plots for both species, except for *A. sterilis* seedlings in plot 1. The nugget effect for *A. sterilis* in plot 1 was about 86% (Table 3). However, once data were detrended, the level of non-structural variation rose above 50% in all plots for both species, except for *L. rigidum* in plot 4, in which the nugget effect was still about 46% (Table 3).

Both species had hole effects and zonal anisotropy in one or another plot (Fig. 3). However, there were differences in the patterns displayed by each species. *L. rigidum* population had a characteristic periodical pattern in three out of the four plots, with a clear hole effect at approximately 5 m in the 0º direction (Fig. 3J-L) and less evidently in the adjacent 45º and 135º directions (data not shown). *A. sterilis* population lacked the characteristic periodical pattern except in plot 2 (Fig. 3B). All other plots showed a monotonically increasing pattern, with longer ranges in the 90º direction, regardless of the percentage of variability explained by the spatial pattern (Fig. 3A, 3C, 3D).

However, zonal anisotropy was greatly reduced or absolutely erased when the analyses were performed on the detrended data. The data only failed to remove zonal anisotropy in plot 1 for *A. sterilis* detrending (Fig. 3F). Geometrical anisotropy and hole effects were also largely removed from experimental semivariograms with detrending by the median polish algorithm.

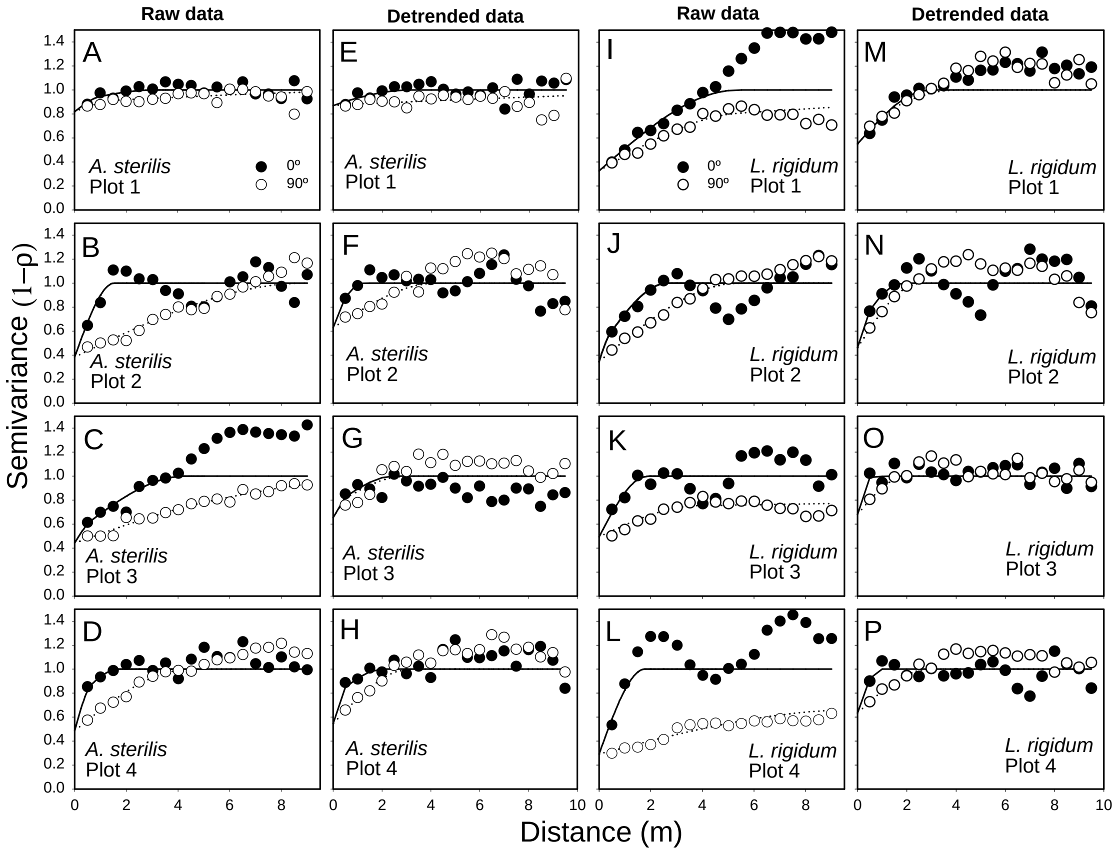

Fig. 3 Fine-scale spatial structure for *Avena sterilis* (left) and *Lolium rigidum* (right) in each of the plots. Symbols indicate the values of the experimental semivariograms and the lines represent the model fit by weighted least squares. Dots (●) represent the 0º (across crop rows) direction, and circles (○) represent the 90º (parallel to crop rows) direction.

3.4. Spatial stability of populations

The Syrjala test did not reveal any spatial stability of populations across years for *L. rigidum* or *A. sterilis* (Table 4). All experimental coefficients yielded a *P*-value lower than 0.05, indicating that the spatial distribution of populations was statistically different between years. However, each species correlated with its own population of the previous year to some degree (Table 5). Correlation extended no further than one year for *L. rigidum*. Moreover, *L. rigidum* showed an important reduction in correlation between the 2002 and the 2003 populations (from $\rho_{2001\text{-}2002} = 0.508$ to $\rho_{2002\text{-}2003} = 0.214$). *A. sterilis* had higher correlation between years in both periods ($\rho_{2001\text{-}2002} = 0.812$ and $\rho_{2002\text{-}2003} = 0.746$); in addition, this correlation extended from the first to the third year ($\rho_{2001\text{-}2003}$ = 0.596). These inter-year relationships are also found in the analysis of the detrended data (Table 5).

Table 3 Correlogram parameters for *Avena sterilis* and *Lolium rigidum* in each of the plots at fine-scale, as estimated by weighted least squares from the log-transformed (raw) data and the median polish (detrended) data.

	c_0	c_1	a_{1max}	a_{1min}	α_1	c_2	a_{2max}	a_{2min}	α_2
Raw data									
A. sterilis									
plot 1	0.86	0.04	7.99	2.52	118.80	0.10	1182.52	2.80	84.64
plot 2	0.39	0.52	10.73	1.54	93.87	0.10	10.27	1.56	93.08
plot 3	0.45	0.47	13.02	4.51	106.47	0.08	917.64	0.61	89.58
plot 4	0.49	0.23	338.23	0.64	100.28	0.28	6.58	1.69	81.23
L. rigidum									
plot 1	0.34	0.30	713.35	5.46	100.70	0.36	6.30	5.20	171.07
plot 2	0.40	0.20	11.58	2.33	109.46	0.41	15.24	2.25	18.30
plot 3	0.43	0.28	6774.02	2.35	90.00	0.28	3.20	1.10	90.62
plot 4	0.28	0.40	2897.14	1.74	90.00	0.32	12.26	1.76	86.31
Detrended									
A. sterilis									
plot 1	0.87	0.12	45.26	3.05	97.07	0.01	4464.54	0.00	145.55
plot 2	0.63	0.16	5.50	0.91	98.29	0.21	5.38	1.07	99.14
plot 3	0.65	0.10	0.45	0.42	156.11	0.25	3.20	2.37	117.60
plot 4	0.55	0.23	209.33	0.56	100.71	0.23	3.45	2.02	76.17
L. rigidum									
plot 1	0.55	0.15	2.96	1.82	0.00	0.30	4.38	2.73	68.00
plot 2	0.46	0.39	4.60	1.50	123.25	0.15	4.04	0.27	94.61
plot 3	0.68	0.30	1.89	0.45	90.00	0.02	2.37	1.31	88.39
plot 4	0.63	0.19	2.94	0.70	92.48	0.18	3.78	0.99	103.65

See Table 2 for further details on symbols.

Table 4 Syrjala test statistic (*Ψ*) and its level of significance for the difference in the spatial distribution of populations of *Lolium rigidum* and *Avena sterilis* between pairs of years. *** $P \leq 0.001$.

	2002	2003
A. sterilis		
2001	0.376^{***}	2.232^{***}
2002		0.789^{***}
L. rigidum		
2001	1.125^{***}	2.387^{***}
2002		0.424^{***}

Table 5 Pearson correlation coefficient for *Lolium rigidum* and *Avena sterilis* densities throughout the three years. The correlation coefficient was computed on the log-transformed data (raw data) and on the residuals from the median polish algorithm (detrended data). $^{*}P \leq 0.05$, $^{**} P \leq 0.01$, $^{***} P \leq 0.001$.

	L. rigidum			*A. sterilis*		
	2001	2002	2003	2001	2002	2003
Raw data						
L. rigidum						
2001	1					
2002	0.508***	1				
2003	0.054	0.214**	1			
A. sterilis						
2001	0.306***	0.070	-0.315***	1		
2002	0.296***	0.057	-0.223***	0.812***	1	
2003	0.248***	0.009	-0.138*	0.596***	0.746***	1
Detrended data						
L. rigidum						
2001	1					
2002	0.344***	1				
2003	0.065	0.206**	1			
A. sterilis						
2001	0.097	-0.015	-0.323***	1		
2002	0.025	0.002	-0.269***	0.610***	1	
2003	-0.018	-0.094	-0.166*	0.378***	0.507***	1

The codispersion coefficient analysis gives results according to those of the correlation coefficient. The codispersion coefficient from the comparison of *L. rigidum* densities in two consecutive years yields positive values within the entire domain, except at long distances (>100 m; see Fig. 4F), as well as relatively constant values for all distances. The codispersion coefficient for *A. sterilis* in consecutive years shows a typical “semivariogram” shape, with a more or less steep increase from 0 to 30 m and then a levelling-off (Fig. 4A-C). The codispersion coefficient levels off at different levels, depending on the two years being compared. The “sill” of the codispersion coefficient is about 0.6 between the 2001 and 2002 populations and between the 2002 and 2003 populations (Fig. 4A, C); however, it is about 0.4 between 2001 and 2003 (Fig. 4B).

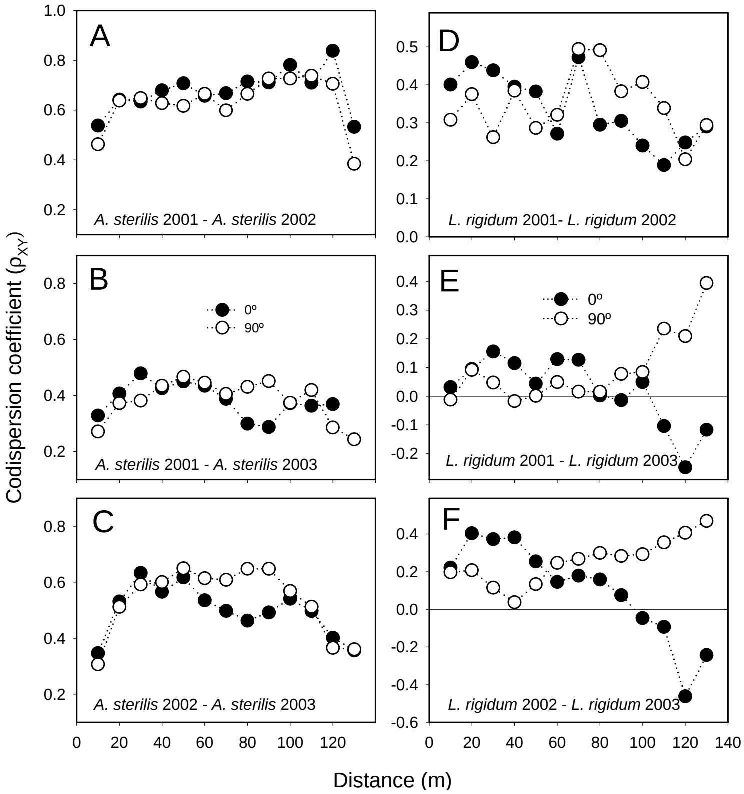

Fig. 4 Codispersion coefficient ρ_{XY} between different years for *Avena sterilis* and *Lolium rigidum* in two perpendicular directions. Dots (●) indicate the 0º (across crop rows) direction and circles (○) indicate the 90º (parallel to crop rows) direction. Note the different scales for the plots.

3.5. Spatio-temporal interspecific relationships

Raw and detrended data yield contrasting results in the analysis of the interspecific relationships (Table 5). On the one hand, raw data analysis revealed a low but significant positive correlation between *L. rigidum* and *A. sterilis* populations in 2001. Moreover, the relationship between the *L. rigidum* population in 2001 and the *A. sterilis* population in subsequent years remained positive and significant. However, detrended data did not show such a relationship; the correlation between detrended *L. rigidum* density in 2001 and *A. sterilis* populations was no longer significantly different from zero. On the other hand, correlation analyses between *L. rigidum* density in 2003 and *A. sterilis* populations showed significant but negative correlation coefficients in all three years. Also, the correlation coefficients remained negative and significant after the data were detrended (Table 5).

The codispersion coefficient analysis showed the same trends as the correlation coefficient. For the *L. rigidum* population in 2001 with the *A. sterilis* populations of all other years, the codispersion coefficient remained erratic and near to zero (Fig. 5) except for long distances in the 0º direction (perpendicular to crop rows), at which the coefficient became positive. The codispersion coefficient showed a clear negative relationship between the *L. rigidum* population in 2003 and the *A. sterilis* populations of 2001, 2002 and 2003 (Fig. 5D-F). The codispersion coefficient for all three comparisons decreases gradually for about 40 m, and then shows a hole effect that is stronger in the 0º direction, especially clear when comparing *L. rigidum* density in 2003 and *A. sterilis* density in 2003 (Fig. 5F).

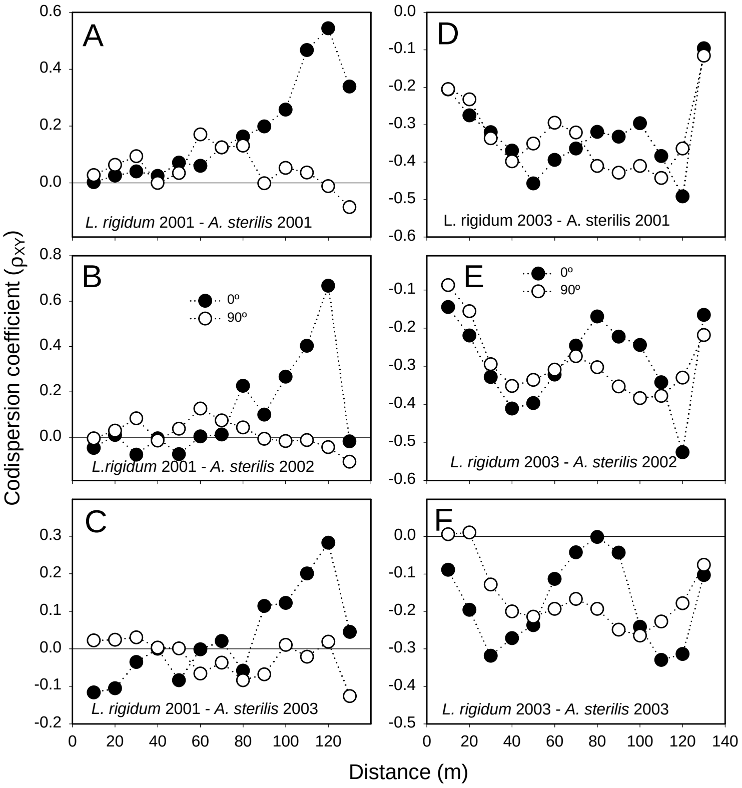

Fig. 5 Codispersion coefficient ρ_{XY} between *Avena sterilis* and *Lolium rigidum* across years in two perpendicular directions. Dots (●) indicate the 0º (across crop rows) direction and circles (○) indicate the 90º (parallel to crop rows) direction. Note the different scales for the plots.

4. Discussion

4.1. Effect of detrending data

One special feature that is sometimes not taken into account in spatial structure analyses is the effect of trends in data on the spatial structure detected. Cardina *et al*. (1995) also looked at trends in the analysis of weed spatial distribution, and observed that results behaved differently, depending on one or another data set. Moreover, detrending might be necessary to filter zonal anisotropy, which in the estimation of semivariogram models is translated into extremely high geometric anisotropy ratios, with ranges up to hundreds or thousands of meters, far exceeding the dimensions of the study site. However, our data detrending still fails to remove completely from the analyses problems such as the presence of zonal anisotropy.

At large scale, detrending is almost completely necessary, since the assumptions that must be met if spatial statistics are to be applied properly (i.e. independence of mean and variance and absence of trends) could not be met. Moreover, the analysis of large-scale variability in weed populations might be strongly influenced by the general slope of the field from SE to NW (Sans *et al.*, 2002) and also by soil and terrain characteristics. This latter feature has been shown for a number of weeds and fields (Andreasen & Streibig, 1991; Cardina *et al.*, 1995; Häusler & Nordmeyer, 1995; Heisel *et al.*, 1999; Clay *et al.*, 2000; Wiles & Schweizer, 2002), and could cause marked large-scale trends in data. Apart from reducing zonal anisotropy effects, detrending also caused a reduction in the ranges of the models, at large- and small-scale descriptions for both species.

Detrending is a powerful tool indeed for describing spatial structure in data. Some authors have considered using only correlograms to describe spatial data (Rossi *et al.*, 1992; Wiles & Schweizer, 2002), since they have the advantage over standard semivariograms of filtering the effects of varying means and variances. Data from our study led us to reject this approach because, in the presence of strong trends or high geometric anisotropy ratios, correlograms perform poorly.

4.2. Large-scale spatial distribution

Our study adds further evidence for the aggregation of weed distribution in agricultural fields. However, since many researchers did not apply any detrending algorithm to their data (Halstead *et al.*, 1990; Clay *et al.*, 2000; Wiles & Schweizer, 2002), it is difficult to compare their results with ours. Moreover, since the ranges and structures detected might depend on field size, weed species and abundance, and sampling design, direct comparison between studies might not be possible.

In our study the spatial structure of each weed is different. *A. sterilis* illustrated that detrending may not be universally useful and desirable, since in this case detrending had no noticeable effect on the analyses: the results of one or another data set were roughly the same. *A. sterilis* showed a fairly similar spatial structure of populations among years at large scale (when compared to *L. rigidum*), and a relatively low nugget effect (low ratio nugget/sill). In addition, geometric anisotropy ratios are moderate, indicating fairly isotropic behaviour of *A. sterilis* populations. Isotropic behaviour of weeds is expected when the dispersal pattern is not affected by directional processes such as wind or the action of farming equipment. This isotropy in population structure may be related to the seed dispersal mechanism of *A. sterilis*. Under Spanish dryland conditions, most seeds are already shed on the ground at harvest time, resulting in minimal dispersal by combines. So, under no wind or inconsistent wind direction during seed shed, dispersal is expected to be roughly the same in all directions. However, the ranges and the directions of maximum continuity do not remain consistent across years, indicating that the phenomena involved in the development of spatial structure may be variable between years, or that the analyses used are unable to reveal clearly the underlying mechanisms of pattern formation.

L. rigidum illustrates how remarkable differences can be obtained from analyses using raw or detrended data. The moderate spatial dependence that the *L. rigidum* population showed in 2001 and 2002, with long ranges in the direction parallel to crop rows (90º) but still longer ranges in the perpendicular direction, leading to effective zonal anisotropy, was caused exclusively by the trend present in data (the mean density increased steadily from East to West). This kind of behaviour might lead to erroneous conclusions about the shape and direction of patches, and about the underlying processes. In these cases detrending allows us to reveal the “true” spatial structure of data. In our case, *L. rigidum* has very limited spatially structured variation at large scale, despite the relatively low nugget effect predicted by the weighed least-squares fitting of the theoretical model. There is no good reason to suppose any spatial structure more than a pure nugget effect, especially in the 2001 *L. rigidum* population (Fig. 2J). This confirms the general reluctance of engineers and other geostatisticians to rely solely on automated procedures to fit models to experimental semivariograms (Pannatier, 1996; Webster & Oliver, 1997; Deutsch & Journel, 1998; Webster & Oliver, 2000). Most *L. rigidum* spatial variability may be lost due to the distance between samples, which may be inappropriate to the aims (Rew & Cousens, 2001; Cousens *et al.*, 2002). However, this is a general problem that weed scientists and agricultural consultants should face, since there is a trade-off between the sampling effort and the information obtained. In fact, as stated elsewhere for seed banks’ spatial variability (Wiles & Schweizer, 2002), if one wants to calculate weed density one should use uncorrelated samples (i.e. the distance between samples should be longer than the estimated range). However, if the main aim is to produce a weed map, correlated observations are needed (so sampling must be closer than the estimated range).

However, the *L. rigidum* population had a completely different spatial structure in 2003, with a well-defined sill beyond 40 m, and a clearly increasing trend of the correlogram at short distances. It is roughly similar to the experimental correlogram obtained for *A. sterilis* in 2003. This question will be developed further when the spatial stability of patches and the relationships between species are discussed.

4.3. Fine-scale spatial distribution

The results obtained from fine-scale raw data tend to corroborate the general idea that the spatial structure detected depends on the sampling scale (Cousens & Croft, 2000; Rew & Cousens, 2001; Cousens *et al.*, 2002). The spatial structure of the two weed populations is different at fine and large scale. Moreover, the spatial structure detected at fine scale does not seem to continue at large scale, indicating that different phenomena are operating at each scale.

Both species show a moderate-to-high nugget effect, indicating that, even at 0.5 m, discrete sampling might reveal processes that are being missed. The nugget effect was only very high in plot 1 for *A. sterilis*, in which its mean density was very low and the population was sparse. There might be an inherent error in sampling seedling populations (error in counting, identification), which could cause a nugget effect when computing the semivariogram. However, even though semivariance description and kriging estimation of weed populations are widely used in the literature (Donald, 1994; Heisel *et al.*, 1996; Colbach *et al.*, 2000a; Cousens *et al.*, 2002), we should bear in mind that weeds behave like point processes, in which there are discrete individuals dispersed in the sampling domain. This is one of the main points that causes uncertainty at shorter scales.

Both species still show more common features than those already noted. Both species show zonal anisotropy in one or another plot (at least in raw data) and a periodical pattern with a hole effect. However, as has been pointed out previously, each species has its own inherent behaviour. Zonal anisotropy occurs in three of the four plots for *L. rigidum*, whilst it only occurs in one plot for *A. sterilis*. Zonal anisotropy indicates the presence of two distinct spatial distributions (Wiles & Schweizer, 2002) or an additional source of variability in one direction, so the sill depends on the direction (Samper & Carrera, 1996). At this fine scale sampling, harvest equipment is the factor that could explain such variability and give such a consistent effect across locations. It could also explain the hole effect present in some plots, especially for *L. rigidum* (Blanco-Moreno *et al.*, 2004). Combine harvesters run across crop fields, catching straw and grain (and weed seeds) from wide swathes, and generate narrow bands of chaff and straw. Thus, the harvest trail and the straw band can be seen as the two different distributions (or the additional source of variability) that we were looking for (Blanco-Moreno *et al.*, 2004).

The dispersal behaviour of both species explains such differences in the fine-scale variability of their populations in relation to combine harvesting. On the one hand, *L. rigidum* does not shed its seeds spontaneously before crop harvest, and even after harvest most seeds are dispersed as clustered spikelets or spike fragments (Recasens *et al.*, 1997). Up to 16% of them may still be attached to broken segments of seed heads

(Gill, 1996a), indicating that seeds seldom fall freely from spikelets without the help of mechanical action. *L. rigidum* seed dispersal is strongly affected by combines, which concentrate its seeds on a narrow strip (Blanco-Moreno *et al.*, 2004). On the other hand, *A. sterilis* has largely shed its seeds on the ground by harvest time under Spanish dryland cereal conditions (Barroso *et al.*, 2004). As it has no adaptations to aid long-distance dispersal, most seeds fall within a 1 m radius of their origin (González-Andújar & Perry, 1995; Medd, 1996a; Shirtliffe *et al.*, 2002). This weed species is less susceptible to a marked effect of combines on its dispersal than *L. rigidum* is.

Nevertheless, *A. sterilis* displayed a clear periodic pattern in plot 2. Plot 2 was in a zone that underwent crop lodging before *A. sterilis* shed its seed, which probably caused the seeds to be retained among leaves and straw of parent plants and the cereal, and so be harvested and dispersed in the same way as *L. rigidum*. The periodical pattern is lacking from the *A. sterilis* population of the remaining zones, since dispersal happened in the usual way.

The effect of detrending data on the spatial structure of both species is mainly the same as at large scale. Detrending reduces the ranges of spatial dependence, lessens the geometric anisotropy ratios and largely erases zonal anisotropy. Nevertheless, it also fades out the hole effect caused by combine harvesting, though not in all plots. The causes of such a variable effect of detrending on the output of geostatistical analyses must be sought in the directions of variation. Since median polish algorithm is performed over rows and columns in a gridded data set, there is no guarantee that it is performed according to the trend directions (Cressie, 1993), since the main directions of the sampling grid may not coincide with the direction of variation. In the case of plots 4 and 5, in which straw swathes from harvest were almost perfectly aligned with the sampling grid, the already apparent periodical pattern in the 0º direction and the clear zonal anisotropy in the 90º direction disappear almost completely.

4.4. Spatial stability of weed populations

Some previous studies reported spatial stability of weed patches under moderate applications of herbicides (Wilson & Brain, 1991; Walter, 1996; Barroso *et al.*, 2004). However, they used different methods, which hinders direct comparisons.

We found no spatial stability such as that measured by the Syrjala test in either weed (Syrjala, 1996; Barroso *et al.*, 2004). In the case of *L. rigidum*, whose populations experienced a formidable increase and became homogeneous across the field from a very unequal distribution, this was reasonable (Fig. 1).

However, *A. sterilis* patches were located almost in the same places year after year, with a gradual increase in density. They were *visually* stable across years, although the Syrjala test failed to detect such positional stability. The Syrjala test is supposed to be unaffected by total amount, since it is a test based on the differences between two cumulative distribution functions that works on standardised values. Moreover, owing to the type of statistic (Cramér–von Mises test), it is supposedly preferable to other types because it is less affected by the presence of a few extreme observations (Syrjala, 1996). Nevertheless, the other measurements of inter-year association give us a different picture. The correlation coefficient for *A. sterilis* between consecutive years is relatively high (above 0.7 for raw data, and above 0.5 for detrended data; see Table 5). The codispersion coefficient is also high (above 0.5) and relatively stable at distances longer than 20 m for the pair 2001-2002 (Fig. 4A) and distances above 30 m for the pair 2002-2003 (Fig. 4C). It is indicative of two spatial distributions that correlate with each other [remember that the codispersion coefficient should go towards the correlation coefficient as distance approaches infinity (Goovaerts, 1994b; Webster & Oliver, 2000)]. The codispersion coefficient follows similar trends in both directions, indicating approximately the same degree of relationship regardless of direction. Interestingly, this structure appears between pairs of consecutive years and also between non-consecutive years (i.e. 2001-2003, see Fig. 4B), indicating that the same structure of correlation is maintained.

4.5. Spatio-temporal interspecific relationships

The analysis of raw vs. detrended data is also a powerful tool for unearthing the relationship between species. As was previously noted, Pearson correlation analysis gives very different results depending on whether data are raw or detrended. It should be noted that intraspecific relationships remain largely unaltered after detrending, although all correlation coefficients are lowered, but interspecific relationships change, at least for the pair of years under consideration. The *L. rigidum* population in 2001 seemed to correlate positively with the *A. sterilis* population in 2001 and subsequent years. In fact, the weed maps for 2001 (Fig. 1) show that the zones most densely occupied by both species tend to overlap, although there might be an ecological reason for such association. Once the general trend (stronger for the *L. rigidum* population) which runs fairly parallel to the drainage system is removed, the correlation between *L. rigidum* in 2001 and *A. sterilis* is lost. It may be seen as a spurious correlation between the two species.

Nevertheless, the correlation was negative between the *L. rigidum* population in 2003 and *A. sterilis* populations, and it was preserved after detrending. The relationship between *L. rigidum* in 2003 and *A. sterilis* is clearly antagonistic. In those places in which *A. sterilis* population is persistent across time, it may steadily supplant *L. rigidum*. *L. rigidum* is less competitive than *Avena* species (Pannell & Gill, 1994). It may be that, under strong herbicide pressure, competitive relationships (dependent on density) could be masked, as both species tend to be concentrated in certain defined areas prone to higher seed production or less herbicide efficacy. Nevertheless, in our study, in which herbicide application was absent in the first year and may have largely failed the second year, weed populations followed their intrinsic dynamics. Competition could then play a major role in the establishment of hierarchies between species, so that the most competitive species takes on a leading role in the weed community. Intra- and interspecific competition could cause a significant reduction in seed shed by one of the species (*L. rigidum* in our case), which could lead to lowered populations in the following year. This may cause the correlation coefficient to be higher (but negative, Table 5) between *A. sterilis* in 2002 and *L. rigidum* in 2003 than between *A. sterilis* in 2003 and *L. rigidum* in 2003.

4.6. Concluding remarks

We argued in our study that a static picture of weed distribution does not explain the spatial structure of weed populations and the dynamics of patch distribution. Different techniques should be used in spatial structure descriptions to reveal characteristics that could be missed with a single analysis. We also supported the view that spatial analyses should be performed at diverse spatial scales to cover the different sources of variability. The sampling scale required depends on the aims of surveys and the reasons for data collection (Rew & Cousens, 2001; Cousens *et al.*, 2002). The description of the effect of harvesting on weed pattern through its effect on seed dispersal could be adequately studied at a scale of tens of centimetres (although it might also depend on the direction considered, as discussed above), but the effect of competition is best described at the scale of tens of metres –although this may depend on the type of habitat (Coomes *et al.*, 2002)–. It is clear that such time- and effort-consuming descriptions are not practical in recommendations to farmers. However, from the common results of diverse studies we should be able to extrapolate general rules for optimising sampling designs –for example, accounting for anisotropy (Wiles & Schweizer, 2002)–. Moreover, the joint description of multiple-species assemblies and their evolution over time could provide insights into the main factors in a community's ecology and the role of competition on the distribution of species in agricultural fields.

CHAPTER III

WITHIN-FIELD STABILITY OF WEED DENSITY–CROP YIELD INTERACTIONS IN *LOLIUM RIGIDUM* AND *AVENA STERILIS* ASSEMBLIES

Summary

The study of stable crop yield loss–weed density interactions is considered to be capital for the application of threshold theory. A two year experiment was conducted in three contrasting topographical areas within a single wheat field to determine the stability of the effect of weed mixtures (dominated by *L. rigidum* and *A. sterilis*) across time and location. Weed-free yield varied between locations as well as between years. In one area there was no clear relationship between yield loss and weed density. In the other two areas, however, competition parameters stability was detected, though a change in competitive relationships was observed over years. As has been reported previously, *A. sterilis* was more competitive than *L. rigidum*, and this relationship seems to be stable over time and location. However, *L. rigidum* performed better in the first year, a dry season, whilst its effect is hardly noticeable in the second year, a wetter one. Our findings are discussed in relation to threshold theory in weed control, and the difficulties that this theory could face on implementation.

1. Introduction

Variation in interference relationships at different spatial (i.e. regions, fields) and temporal scales has been shown for a number of crop–weed associations (Lindquist *et al.*, 1996; Cousens & Mokhtari, 1998; Jasieniuk *et al.*, 1999; Lindquist *et al.*, 1999; Moechnig *et al.*, 2003). Such variation in predictions of yield loss from theoretical models is relevant for the development of decision support systems for integrated weed management. However, within-field variation has not been described in depth, a matter that could hinder weed scientists' efforts to determine reliable economic thresholds.

Lolium rigidum Gaudin (annual ryegrass) and *Avena sterilis* L. (wild oat) are two of the most troublesome weeds in Mediterranean dryland crops (González-Andújar & Fernández-Quintanilla, 1993; Gill, 1996b; Medd, 1996b; Recasens *et al.*, 1997). *L. rigidum* can cause important yield reductions in cereal crops (Lemerle *et al.*, 1995; Cousens & Mokhtari, 1998), although its competitiveness is affected by environmental factors such as rainfall and light (Lemerle *et al.*, 1995; Izquierdo *et al.*, 2003). *A. sterilis* is also highly competitive, and its effects on crop yield are noticeable even at low densities (Torner *et al.*, 1991; González Ponce & Santin, 2001).

L. rigidum and *A. sterilis* are particularly problematic for wheat (*Triticum aestivum* L.), one of the most important crops in Mediterranean areas. Many attempts have been made to characterise wheat's performance as a result of competition from *L. rigidum* (Lemerle *et al.*, 1996; Lemerle *et al.*, 2001), and the geographical and temporal variability of this interference (Cousens & Mokhtari, 1998), as well as that from *Aegilops cylindrica* (Jasieniuk *et al.*, 1999). There are also some studies on the competitive ability of *A. sterilis* against wheat (Balyan *et al.*, 1991; González Ponce & Santin, 2001), but they are not so focussed on the variability of interference relationships.

However, as for any weed, interaction between *L. rigidum* and wheat cannot be evaluated accurately without considering other weed species commonly present in the weed community which *L. rigidum* dominates (Hume, 1993; Swinton *et al.*, 1994). An added value of this study emerge from that weed communities of winter wheat crops in north-eastern Spain are usually dominated by *L. rigidum* and *A. sterilis* assemblies, and few broad-leaved weeds are present in such agro-ecosystems. A previous study by Pannell and Gill (1994) on the performance of *Avena fatua* and *L. rigidum* mixtures under controlled conditions highlights the necessity for multi-species models to obtain a realistic picture of the effects of weeds on crop yield. However, in their studies, they controlled weed densities and did not pay attention to the possible variation of competition relationships and crop-yield loss in commercial fields. Moreover, their model tends to overestimate the competitiveness of each weed, as it fails to represent the interaction between weeds, such that their predictions exceeded actual observed yield loss. In relation to mixed weed communities, there are only a few studies that compare competitive relationships across time and location (Swinton *et al.*, 1994; Moechnig *et al.*, 2003), and none until now that address the possibility of changes in competitive relationships within a field.

While many studies have analysed the competitive relationship between wheat and either *L. rigidum* or *A. sterilis*, further research is needed to evaluate the stability of combined wheat–*L. rigidum*–*A. sterilis* interference relationships, especially stability at scales much smaller than the regional scale. This interest in small scale agricultural phenomena has been enhanced by the development of precision agriculture, and several previous works have already explored yield variation within individual fields. Colvin *et al.* (1997) reported that crop yields within a field showed a coefficient of variation ranging from nearly 12% to 30% depending on the year. Taylor *et al.* (2003) reported within field variations from 0.8 to 2.1 t ha^{-1} in UK crops. But in spite of this interest in local variability in agricultural phenomena, there have been few studies addressing the specific issues of competitive relationship variation (for studies on a regional scale see Lindquist *et al.*, 1996, 1999).

Most competition studies analysing single or multi-weed species effects on crop yield have been carried out under experimental conditions (but see Hume, 1993; Swinton *et al.*, 1994). Under natural conditions, variations in biotic and abiotic conditions may pose additional challenges to mathematical descriptions and the modelling of competition output, but offer the advantage of a closer representation of competition in real situations. In this paper we present data from a two-year study examining natural weed-mixture (*L. rigidum* and *A. sterilis*) interference on wheat yield, and determine whether yield loss caused by this weed assembly is stable across locations within a field and interannually.

2. Materials and methods

2.1. Field site and operations

We carried out our study in a 8 ha field located in Calonge de Segarra (Central Catalonia, north-eastern Spain, 41º45’32” North 1º31’29” East). The field had been sown with wheat during the previous years (from 1999 to 2002) and infested predominantly with *L. rigidum*, although some well-defined zones had low infestations of *A. sterilis*.

The field is topographically irregular with differences in elevation of up to 10 m, though it all falls within a single drainage system, running from the south eastern corner to the north western corner. The soil texture of the field ranged from loam to clay loam. Rainfall and temperatures were obtained from the nearest meteorological station, which was located in Pinós, about 7 km to the north.

Table 1 Mean topographical characteristics of each area.

area	Slope (%)	Aspect (deg.[*])	Elevation (m[**])
1	7.69	223.60	1.50
2	5.12	274.51	5.15
3	7.25	176.07	9.96

[*]Aspect is measured in degrees clockwise from north. [**]Elevation is the difference in metres to the lowermost sampled point.

We selected three areas for comparative purposes. Three equally sized field areas measuring 31 m × 51 m (which will be referred to as areas 1, 2 and 3) were selected to represent contrasting topographical positions (Table 1). We selected areas that had minimally sloping surfaces, but nowhere was completely flat in the field. They also differed slightly in aspect. Although the infestations of *L. rigidum* and *A. sterilis* were unequal at the beginning of the study (Table 2), the range of weed densities in each of the three areas was nevertheless sufficient to permit statistical analysis.

Table 2 Mean (± standard error) weed density of each area in the first and the second year.

	First year		Second year	
	density (pl m^{-2})			
area	**ryegrass**	**wild oat**	**ryegrass**	**wild oat**
1	816.2 ± 121.1	3.3 ± 1.4	2343.4 ± 210.6	20.8 ± 9.0
2	655.1 ± 117.2	42.0 ± 9.7	1722.8 ± 160.6	124.5 ± 21.9
3	194.0 ± 36.1	2.2 ± 1.0	1212.0 ± 133.6	6.6 ± 2.5

The field was ploughed each year (on September 15th 2000 and September 19th 2001) and the seedbed prepared a month later (on October 19th 2000 and October 19th 2001), before sowing. The farmer seeded with his own seeding equipment, and the entire field was sown with wheat (*Triticum aestivum* cv. Soissons) at a density of 180 kg ha^{-1} (approx. 400 grains m^{-2}), on November 3rd 2000 and November 8th 2001. Fertiliser was added twice; a granular application of NPK 10-15-15 at 325 kg ha^{-1} before sowing and a liquid application of SN32 (Urea-Nitrate-Ammonium) at a rate of 280 kg ha^{-1} in the winter (February 9th 2001 and February 20th 2002). A mixture of herbicides to control broadleaf weeds (chlorsulfuron at 9 g.a.i. ha^{-1} plus tribenuron-methyl at 9.375 g.a.i. ha^{-1}) was applied both years. To ensure measurable populations of the target weed species, no grass weed herbicide was used in the first year. However, a grass weed herbicide (diclofop-methyl at 350 g.a.i. ha^{-1}) was applied the second year in order to prevent a large increase of weed populations.

2.2. Sampling

24 plots of 1 m × 1 m, 9 m apart were delimited within each area. The plots were georeferenced using a submetre accuracy Ashtech G-12 (Magellan Corporation, Santa Clara, California, USA) differential global positioning system (DGPS) to ensure accurate re-localisation between years, and marked with canes to facilitate measurements during the growing period.

Density was evaluated on 7th and 8th January 2001, and on 30th and 31st January 2002. Because of the high weed density and the sub-metric spatial variability of the *L. rigidum* population, we sampled nine 10 cm × 10 cm quadrats, randomly placed within each 1m × 1 m plot to increase support for density observations. *A. sterilis* density was evaluated in four 25 cm × 25 cm quadrats both years, because of its larger seedling size and lower density compared to *L. rigidum*. Weed density was assumed to be fairly constant throughout the growing season, so plants were not counted again afterwards (Fernández-Quintanilla *et al.*, 2000). Crop biomass data was collected at maturity on 7th July 2001 and 10th July 2002, before harvest. Wheat yield was measured by harvesting by hand four 25 cm × 25 cm quadrats, randomly selected within each 1 m × 1 m plot. These 25 cm × 25 cm quadrats were aligned with a wheat row so that the same number of wheat rows was contained in each quadrat. Biomass was then oven dried for 24 h at 60ºC and weighed.

To have a measure of potential crop production in each area, crop yield in weed-free areas was assessed in independent plots. Six additional plots, measuring 50 cm × 50 cm, were regularly placed within each area. In February plots were treated with diclofop-methyl at 712 g.a.i ha^{-1}, to avoid interference from weeds. Wheat yield in these plots was also measured at maturity by harvesting the plots by hand. Biomass was oven dried for 24 h at 60ºC and weighed. Although there was no evidence of any phytotoxic impact on the crop, other trials indicate that diclofop-methyl typically reduces wheat yields to some degree (Pannell, 1990). Thus it is possible that potential yield could be biased downwards. The mean potential yield obtained from these weed free plots was then used to calculate yield loss for each of the 24 plots, since we expected negligible differences in weed-free yield within each of the three areas.

The second year, high rainfall after herbicide application led to a wash off and a lack of herbicide effect on weed-free plots. Thus, the maximum yield of each area was inferred from those plots presenting the minimum joint weed (*A. sterilis* and *L. rigidum*) infestation and maximum wheat biomass (Jasieniuk *et al.*, 1999). Therefore, potential yield may also be biased downwards and yield losses upwards. Nevertheless, upwardly biased yield loss predictions are a lesser problem because, from a farmer’s perspective, it is better that a model makes cautious management recommendations (Jasieniuk *et al.*, 1999) than underestimating the effects of weeds.

2.3. Data analysis

Crop yield loss–weed density relationship have traditionally been described by means of the model proposed by Cousens (1985):

$$crop\ yield\ loss = \frac{Iw}{1 + Iw/A} \tag{1}$$

in which *w* is weed density, *A* is the maximum yield loss (asymptotic yield loss) and *I* is the yield loss per weed unit as weed density approaches zero (initial slope). The statistical strengths of this model are widely accepted (Cousens, 1985; Kropff & Spitters, 1991; Pannell & Gill, 1994; Swinton *et al.*, 1994), even though this kind of equation (two parameter rectangular hyperbola) is characterised by rather poor estimation properties (Ratkowsky, 1990). Nevertheless, its simplicity and biologically plausible functional form have favoured it over many other more complex models (Cousens, 1985).

Variations have been postulated to model the effects of multi-species weed assemblies on crop yield (Pannell & Gill, 1994; Swinton *et al.*, 1994). Swinton *et al.* (1994) proposed a reformulation of the rectangular hyperbola to take into account any additional weed species:

$$crop\ yield\ loss = \frac{\sum_i I_i w_i}{1 + \sum_i I_i w_i / A} \tag{2}$$

where w_i denotes the density of the i^{th} weed species, I_i the initial slope for that species (in our case I_r for *L. rigidum* and I_o for *A. sterilis*), and *A* is the maximum yield loss.

Pannell and Gill (1994) proposed another variation of the basic model in which crop yield loss from weed mixtures was modelled in a fairly independent way for each weed species:

$$yield = y_{wf}\left[1-\frac{I_1 w_1}{1+I_1 w_1/A_1}\right]\left[1-\frac{I_2 w_2}{1+I_2 w_2/A_2}\right] \tag{3}$$

in which y_{wf} is the crop yield in the absence of weeds, and all other parameters are the same as in equation (2), except for A, which is independent for each weed species. All parameters are estimated jointly, such that yield loss from one species is a fixed proportion of the yield following competition with another weed. This model has the advantage of considering that the total crop yield loss caused by one species (A_i) can be different from the total yield loss caused by another one, instead of considering maximum yield loss to be a fixed proportion independent of species, as in equation (2).

Both models were evaluated to describe the data presented here; crop yield data for each year and location was fit using the Marquardt least squares estimation method with SAS non linear regression procedure (SAS, 1999). Equation (2) provided marginally better results (slightly higher adjusted-R^2, better convergence) and offers the advantage of being simpler because only one parameter has to be estimated for each weed species included in the model, as opposed to two.

Estimated competition curves were tested for significance by means of an approximate F-statistic (MSR/MSE) (Jasieniuk *et al.*, 1999); when neither the hyperbolic nor any linear fit were significant the data set was excluded from subsequent tests. When regression was significant and error variance between data sets was homogeneous (Lindquist *et al.*, 1999), the extra sum of squares principle (hereinafter referred to as ESS) for regression analysis comparisons was employed to evaluate equality of estimated parameters among data sets (Ratkowsky, 1983). ESS has been described in depth by Ratkowsky (1983), and used for comparing non-linear models applied to crop yield loss studies, with some variations (Lindquist *et al.*, 1996; Lindquist *et al.*, 1999; Moechnig *et al.*, 2003). The ESS procedure is based upon the significance of the difference in the residual sum of squares (RSS) between models by means of an approximate F-statistic:

$$Variance\ ratio = \frac{\left((RSS_b - RSS_a)/(df_b - df_a)\right)}{RSS_a / df_a} \tag{4}$$

which measures the increase in RSS in relation to the increase in degrees of freedom of residuals (*df*) when comparing any model (*b*: null hypothesis, “there is one model which describes adequately all data sets being compared”) to the most complex model (*a*: alternative hypothesis, “there is a different model for each data set being compared”). The null hypothesis (whatever it is) is rejected if this variance ratio is larger than the critical F value ($F_{\text{df numerator, df denominator, } \alpha = 0.05}$).

ESS can be summarised in a series of steps:

1. Fit equation (2) to each data set to be compared independently and pool the residual sum of squares, or, alternatively, all parameters may be estimated in a single estimation by minimising:

$$RSS_A = \sum_{i=1}^{n}\sum_{t=1}^{m}\left(yl_t - \left(I_{ri}r_t + I_{oi}o_t\right)/\left(1 + \left(I_{ri}r_t + I_{oi}o_t\right)/A_i\right)\right)^2 \tag{5}$$

in which *i* represents one data set from the *n* data sets to be compared, *m* is the sample size of the i_{th} data set and *t* represents an observation in the i_{th} data set. r_t is *L. rigidum* density and o_t is *A. sterilis* density for observation *t*. yl_t is the measured yield loss for observation *t*. All other parameters are as described in equation (2).

2. Fit a common I_r, I_o and *A* to all data sets to be compared. This involves minimising the sum of squares:

$$RSS_B = \sum_{i=1}^{n}\sum_{t=1}^{m}\left(yl_t - \left(I_r r_t + I_o o_t\right)/\left(1 + \left(I_r r_t + I_o o_t\right)/A\right)\right)^2 \tag{6}$$

Note that the *i* subscripts from equation (5) have disappeared, indicating that the same parameter estimates are used for all data sets. Comparison of RSS_B versus RSS_A allows us to test the null hypothesis that the I_r, I_o and *A* coefficients do not vary among data sets. Rejection of this null hypothesis indicates that I_r, I_o or *A* were different between data sets, but does not indicate which one.

3. Fit a common I_r to the data sets to be compared, whilst allowing I_o and *A* to be different. This involves minimising the sum of squares:

$$RSS_C = \sum_{i=1}^{n}\sum_{t=1}^{m}\left(yl_t - \left(I_r r_t + I_{oi}o_t\right)/\left(1 + \left(I_r r_t + I_{oi}o_t\right)/A_i\right)\right)^2 \tag{7}$$

Note that only the *i* subscript from I_r is lacking, indicating that this parameter gets the same value across data sets, whilst all others are individual to each data set. Comparison of RSS_C versus RSS_A allows us to test the null hypothesis that the I_r parameter varies among data sets. Rejection of this null hypothesis indicates that I_r is different among data sets. This third step is repeated for each other parameter in equation (2), testing whether the observed parameter varies or not among data sets.

Unlike Lindquist and collaborators (Lindquist *et al.*, 1996; Lindquist *et al.*, 1999), we first performed ESS to test the stability of competition effects across space, as small scale spatial variation (hundreds of metres) was expected to be smaller than temporal variation, especially in systems which undergo strong inter-annual variation such as Mediterranean climate regions (Izquierdo *et al.*, 2003). When competition parameters were consistent between locations, the data for those locations were pooled to test stability of competition parameters between years.

3. Results

3.1. Rainfall and temperatures

Rainfall and temperatures during the growing season were somewhat different for each year (Fig. 1). Although cumulative rainfall from October to June was rather similar between years (first year: 371 mm; second year: 400.8 mm), its distribution during the growing period differed.

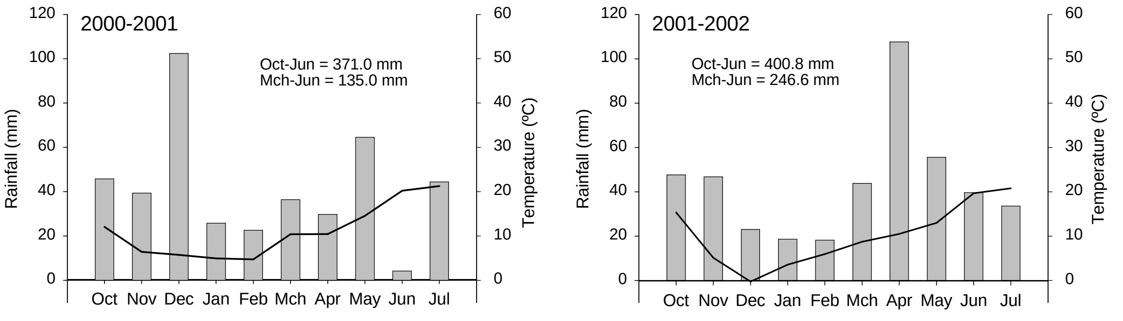

Fig. 1 Monthly cumulative rainfall and mean temperature during the first and second years of the study period.

Only 135.0 mm of rain accumulated from March to June in the first year, whilst in the same period of the second year there was 246.6 mm. Moreover, the mean temperature from December to the end of January of the second year was lower than that of the first year, such that neither the crop nor weeds began to grow until February, when temperature conditions were milder and rain begun.

3.2. Weed density and crop yield differences between areas

At the beginning of the study, weed densities were fairly unequal between areas –differences were up to 20 fold in *A. sterilis* and up to four fold in *L. rigidum* populations (Table 2)–. The second year *L. rigidum* densities homogenised across space because of the lack of grass weed herbicide application during the first year, although there were differences up to twofold in *L. rigidum* densities between area 1 and 3. Meanwhile, differences in *A. sterilis* densities between areas were fairly constant –up to 20 fold both years, despite a conspicuous increase in *A. sterilis* populations.

Table 3 Mean (± standard error) potential crop yield (y_{wf}), estimated from weed free plots, and crop yield at harvest for each area in the first and second year.

	First year		**Second year**	
	crop yield (g m^{-2})			
area	y_{wf}	**wheat**	y_{wf}^{*}	**wheat**
1	1374.5 ± 98.3	661.0 ± 79.1	2035.6 ± 27.2	1644.4 ± 67.5
2	879.7 ± 106.6	516.3 ± 42.4	1277.2 ± 103.2	879.3 ± 71.6
3	632.7 ± 91.54	653.6 ± 39.0	1808.0 ± 16.8	1511.0 ± 52.6

y_{wf}^{*} denotes that weed free crop yield in the second year was not estimated directly from weed free plots. See text for further details.

Mean crop yield including weedy and weed-free plots for each year are summarised in Table 3. Although mean wheat yield was rather similar between areas (610.3 g m^{-2}, CV 13.35%) in the first year, in the second year differences between areas were more conspicuous (1344.9 g m^{-2}, CV 30.39%). There were also marked differences in weed-free yield between areas and between years. As a general trend, all areas showed increased potential crop yield in the second year (up to 150% more in area 3). Area 1 was consistently more productive both years (differences the lowest weed free yield area ranged from 117% in the first year to a 84% in the second one); the differences between areas 2 and 3 were not as significant.

3.3. Weed density–crop yield relationships

The relationships between crop yield loss and weed density for each species, each year and each area are shown in Fig. 2. Crop yield loss is presented as a fraction for each weed so as to make interpretation easier. Equation (2) did not provide a satisfactory fit for area 3 for either year, but neither did linear regression (first year: F = 0.54, P = 0.47; second year: F = 1.59, P = 0.23). Due to this lack of relationship between crop yield loss and weed density in area 3, this data set was excluded from subsequent statistical analyses.

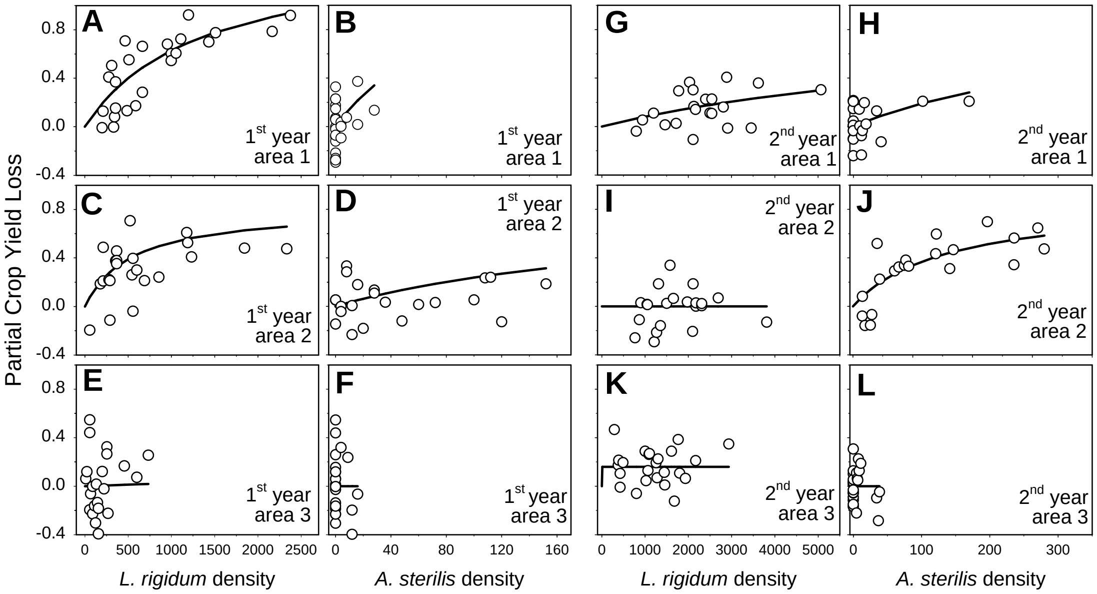

Fig. 2 Partial yield loss caused by each weed species for all three zones and both years. Circles represent observed values and lines are best-fit lines generated from Equation 2 individually for each plot and year.

The relationship between crop yield loss and weed density of each species for each year was satisfactorily described by equation (2) in areas 1 and 2. The approximate F values were significant ($p < 0.001$) in each year for the model describing wheat yield loss based on weed densities. The fit was better for area 1 in the first year (adjusted R^2 = 0.63125) than in the second (adjusted R^2 = 0.20086); whereas for area 2 it was better in the second year (adjusted R^2: 0.65387) than in the first (adjusted R^2: 0.38419).

3.4. Stability of competition between areas

Since regression analyses were significant for areas 1 and 2 in both years and error variance among data sets within each year was constant, tests for spatial stability of parameters could be performed.

All three null hypotheses, testing whether I_r, I_o and A were equal between areas for a given year, were accepted (Table 4); indicating that none of these parameters varies at such a small spatial scale. I values (wheat yield loss as weed densities approach zero) were similar between areas for a given year, as indicated by P-values from the ESS test (Table 4), but the I_o values were higher than I_r both years.

Table 4 Parameter estimates for each area each year (with their standard errors) and *P*-values from difference tests between areas.

	parameter	**area 1**	**area 2**	***P*-value of test**
First year	**all**			0.1419
	I_r	0.0011 (0.0003)	0.0014 (0.0006)	0.6387
	I_o	0.0158 (0.0124)	0.0029 (0.0035)	0.2931
	A	1.4678 (0.4313)	0.8151 (0.2162)	0.16465
Second year	**all**			0.3407
	I_r	0.000131 (0.000069)	0.000013 (0.000105)	0.2865
	I_o	0.0032 (0.0043)	0.0101 (0.0057)	0.3929
	A	0.6778 (0.6277)	0.7670 (0.1638)	0.8909

3.5. Stability across years

To test the stability of parameters across years, data from different locations was pooled for each year, as there was no evidence for spatial differences. The results from the ESS procedure are summarised in Table 5.

I_r varies significantly ($P < 0.0001$) between years (being higher in the first year), indicating that the competitiveness of *L. rigidum* varies over time. However, whilst I_o is higher in the second year than the first, there being a markedly higher effect of *A. sterilis* on the crop, the difference is not significant. suggesting that the effect of *A. sterilis* on wheat yield is rather stable across years. Our results also indicate there were no significant differences in asymptotic yield loss (A) between years.

Table 5 Parameter estimates for each year (with their standard errors) and *P*-values of difference tests between years.

parameter	first year	second year	*P*-value of test
all			0.0000
I_r	0.00129 (0.00026)	0.00010 (0.00003)	0.0000
I_o	0.0016 (0.0018)	0.0058 (0.0030)	0.1557
A	1.1108 (0.1848)	0.8967 (0.3032)	0.5636

4. Discussion

4.1. Weed density–crop yield relationships

In certain areas of the studied field, we failed to detect a clear response in crop yield to weed pressure. Lack of yield reduction from competition with weeds has been shown for other weed species (Bussler *et al.*, 1995; Lindquist *et al.*, 1995). Some authors have also found a lack of fit in situations where crop yield loss was low (van Acker *et al.*, 1997; Moechnig *et al.*, 2003). However, in our case, differences in yield between plots were up to 80% (maximum and minimum in the first year: 1145.6 kg/ha and 287.2 kg/ha; in the second year: 2034.8 kg/ha and 965.2 kg/ha). These results might indicate that there are many other factors that interact with biotics to hinder the interpretation of results.

One possible explanation for the lack of a relationship between crop yield loss and weed density could be water availability. Area 3 is the uppermost zone of the field, characterised by a moderate, slightly south-facing slope (Table 1). Based on inference from slope and aspect calculations (Sharratt *et al.*, 1992), this topography may cause differences in received solar radiation of between 5 and 9%. Higher radiation can lead to overheating and an increase in water deficit in the late growing season, especially in a dry season as the spring of the first year. Moreover, the topographical position of area 3, almost the highest area of the field, and the slope, might increase erosion and soil loss and consequently might decrease water holding capacity (van Wesemael *et al.*, 2003).

Another factor which may have prevented a significant relation between weed density and crop yield is the shortness of the weed density gradient in the area in the first year. *L. rigidum* density ranged from 11 to 733 plants m^{-2}; whilst *A. sterilis* was not present at 19 out of 24 samples. When the gradient used in regression is too short the response of the dependent variable may be masked by overdispersion of data or may simply remain undetected (Cousens, 1985). However, the lack of relationship during the second year, when weed density here rose to levels similar to other areas (ranging from 289 to 2933 plants m^{-2} for *L. rigidum* and from 0 to 38 plants m^{-2} for *A. sterilis*), remains unexplained. Pannell and Gill (1994) report 30% maximum crop yield loss (*A* parameter) for *L. rigidum*, at about 400 plants m^{-2}, which is far lower than the weed density we observed. These striking results suggest that further research is needed to evaluate environmental conditions that result in a failure to detect interference from *L. rigidum* and *A. sterilis* in wheat.

With regards to areas 1 and 2, the poorer fit of models in some situations is difficult to attribute to a single factor. The high dispersion of data, given this was not a controlled experiment, may be the main reason for poor fit (weed density was not controlled, only measured; soil may not have been as homogeneous as thought to be; wheat may not have been uniformly seeded by the farmer's seeding equipment).

Our results from competition coefficients for each species agree with those obtained by Pannell and Gill (1994) for competition coefficients in mixtures of *L. rigidum* and *Avena fatua*, although differences between species were not as high as in our results. Since there has been no comparative study between *A. sterilis* and *A. fatua*, it is difficult to ascertain whether these differences are attributable to different experimental conditions or just to differences between species. Our I_o values also agree with those of Torner *et al.* (1991), though they investigated the interaction between *Avena sterilis* and barley. Torner *et al.* reported yield losses equivalent to I_o ranging from 0.00124 to 0.00435.

The values of I_r (yield loss as *L. rigidum* density approaches zero) are within the range of those previously reported for *L. rigidum* in competition with wheat (Pannell & Gill, 1994) and in competition with barley (Izquierdo *et al.*, 2003). In spite of the available data, it is difficult to evaluate the extent of the stability of I_r, since environmental and experimental conditions vary between studies.

Asymptotic yield loss (*A*) values are also within the range of values previously reported (Pannell & Gill, 1994; Lemerle *et al.*, 1995; Izquierdo *et al.*, 2003). Only the individual value of *A* for area 1 in the first year is unusually high, exceeding theoretical limits. However, unconstrained non-linear regression often produces these kinds of results when observations show substantial variability or the functional shape is ill-defined.

4.2. Stability of competition between areas

Our results indicate that crop–weed competition relationships do not vary, at least within a given field. None of the parameters examined varied between areas. It is plausible that the lack of between-location differences for asymptotic yield loss for either year can be attributed to the low reliability of *A* estimates, owing to data scarcity at higher weed densities for both species (Cousens, 1985). However, I_r and I_o were also rather constant across space (Table 4). This is unsurprising, as competitive relationships are not expected to change within a field unless differences in soil texture or topography are very marked. In our study field the differences in soil texture and topography are too small to affect the competitive relationships between species. Only at a larger scale (between states, between fields in different landscapes or areas comprising different soil series) would one expect such kinds of variation, due to soil type, or environmental and climatic characteristics of the site (Firbank *et al.*, 1990; Cousens & Mokhtari, 1998). Because of such differences in crop yield–weed density relationships, predictions of crop yield at a given density are likely to be imprecise unless the effects of soil type and environment (climate) are included in the model.

The stability of competitive relationships is the complement to yield stability that must be met if we want to establish precision farming practices confidently. Threshold theory considers that weed population effect is size dependent and, as such, allows to predict the consequences of control decisions (Coble & Mortensen, 1992). But if weed density–yield loss relationships are not stable within a field, all efforts in modelling would be in vain. In our study, given that competitive relationships are stable across the field (except for area 3, which we have excluded from this analysis), management practices would depend only on the prediction of yield loss. Yield loss can be forecast using common competitive parameter estimates for all the field but locally varying yields. Crop yield potential would limit the zones where precision farming can be applied. So the main factor in the definition of management zones would involve a previous identification of crop yield potential. At this point, estimates of weed-free crop yield and crop price are still necessary for the implementation of precision agriculture.

However, some authors have reported within field variation of crop yield (Colvin *et al.*, 1997; Taylor *et al.*, 2003), as we, to some extent, have also found (Table 3). As our study shows, maximum crop yield differences between areas were about 1400 kg/ha in the first year (a dry year) and about 600 kg/ha in the second year (a wetter year). Weed-free yield under field conditions may be highly dependent on soil attributes, such as water holding capacity, soil texture or structure, nutrients, etc. (Earl *et al.*, 2003; Taylor *et al.*, 2003), aside from the individual characteristics of the crop. Many precision farming scenarios are based on the assumption of stable yield pattern within a field (Colvin *et al.*, 1997), but short periods of observation do not allow one to assess yield stability confidently, and it is somewhat premature to state that yield is homogeneous across a field based on our results.

4.3. Competition stability across years

Concerning inter-annual stability of competition, some other authors have obtained similar results, reporting between-year stability for maximum yield loss for corn–velvetleaf (Lindquist *et al.*, 1996) and corn–foxtail (Lindquist *et al.*, 1999) interference. Such results are common when the residual dispersion of data is too high, making it impossible to detect differences, but also when the weed density gradient is too short to estimate confidently the value of parameter A (Cousens, 1985). This causes high standard error values for A and thus a failure to detect differences.

However it is somewhat surprising that, independent of weed-free crop yield which has been shown to vary within fields and between years, the level of maximum yield loss is stable across time and space. This stability suggests that there is a yield loss limit associated with weed density that cannot be surpassed, regardless of crop growth or environmental restrictions, at least within the reasonable limits imposed in our study.

Lindquist *et al.* (1996, 1999) offer contrasting results for different weed–crop combinations. They showed that the effects of velvetleaf and foxtail may or may not be stable across years, depending on field site and years being compared. Between-year variation in crop-weed relationships may result from variation in the relative time of emergence of crop and weed, from differential response of crop and weed to different environmental conditions across years, from shifts in resource limitation (water or light), from variation in crop density, and from other management practices.

In our study, the effect of *L. rigidum* in the second year may have been mitigated by rain and thus water availability (Fig. 1). If soil water had not been a limiting factor, light would likely have been the primary cause of yield reduction. Lemerle *et al.* (1996) have shown that the crop attributes most strongly correlated with the competitive ability of wheat against *L. rigidum* in South Eastern Australia are plant height, the number of tillers, early biomass production and leaf size, all of them related to shading ability. *L. rigidum* plants are generally shorter and less vigorous than wheat, suggesting that crop yield reduction would be minimised when there are no water restrictions (a wet year, with soil with high water holding capacity) if wheat and *L. rigidum* plants emerge roughly simultaneously. Competition by *L. rigidum* for water may play a leading role in reducing wheat yield in normal to dry years or in soils prone to water stress (low water holding capacity), whilst without water stress, wheat yield loss caused by *L. rigidum* might be minimal.

Moreover, *A. sterilis* is more competitive than *L. rigidum* and this relationship is also stable across years. In fact, *A. sterilis* has been reported to be one of the most competitive weeds in a wide range of crops (Nietschke & Medd, 1996), and it can cause severe yield reductions (Martin *et al.*, 1987; Nietschke & Medd, 1996; Dhima *et al.*, 2000; González Ponce & Santin, 2001). However, *A. sterilis* is known to be affected by drought to a greater extent than wheat (González Ponce & Santin, 2001). Thus the lack of effect of *A. sterilis* on yield loss in the first year could be a result of differential effects of water stress on wheat and wild oat. In the second year, when no water stress was detected (or its effect was minimal) throughout the growing season, this weed takes on an important role in crop competition. Some areas also experienced an important increase of *A. sterilis* population (Table 2) contributing to a still more marked effect of *A. sterilis* on crop yield, especially in area 2. *A. sterilis* is an extremely aggressive weed, which has high tillering capacity, rapid foliar extension and is also taller than some wheat varieties (straw of cv. Soissons is short and stiff).

Also the conjoint effect of wheat, with no water restriction, and of *A. sterilis* might outcompete *L. rigidum*. Thus the competitiveness of *L. rigidum* almost disappeared in the second year, and its effect on crop yield is minimal. This result reinforces the necessity for conjoint estimation of competitive coefficients in weed mixtures (Hume, 1993; Swinton *et al.*, 1994; Cowan *et al.*, 1998; Moechnig *et al.*, 2003) as well as emphasising the importance of minimising contamination by extraneous weeds in competition trials (Pannell & Gill, 1994). Estimating competition coefficients separately for each species would lead to an overestimation in the measured competitiveness and in consequence biased recommendations on treatments. At the same time it suggests that care must be taken before applying uncritically the same economic threshold criteria in different years. Under a risk aversion perspective it would lead to an extremely conservative strategy that would mean zero density threshold (Pannell, 1995).

The question of coefficient stability is central to establishing the usefulness of this approach for bioeconomic models. Some studies have focussed efforts on ascertaining the geographic area within which a given set of coefficients is appropriate (Swinton *et al.*, 1994; Lindquist *et al.*, 1996; Lindquist *et al.*, 1999), and have highlighted the necessity of parameter stability for a model to be useful. We have explored the questions of parameter stability within field, across locations and across years. Our results confirm to some extent within field parameter stability, especially for those parameters related directly to the competitive impact of weeds on crop yield. Weed-free yield might be the main parameter for evaluating economic threshold, because differences determine whether a treatment is worthwhile or not, especially in those areas with low crop yields.

Apart from such considerations on the benefit of precision management practices, it must not be forgotten that competition parameters show low temporal stability for some weeds, whilst other weeds display more stable competitive relationships across years. It must be evaluated to what extent this instability could affect management decisions.

CHAPTER IV

SPATIAL DISTRIBUTION OF *LOLIUM RIGIDUM* SEEDLINGS FOLLOWING SEED DISPERSAL BY COMBINE HARVESTERS

Summary

This paper considers the relationships between the dispersal of seeds and the distribution pattern of an annual weed. A comparative study of seed dispersal by combine harvesters, with and without a straw chopper attached, was established using *Lolium rigidum*, a common weed in Mediterranean cereal crops. Seed dispersal distance was quantified and the relationships between dispersal and fine scale seedling distribution evaluated. Primary dispersal of *L. rigidum* seeds occurs in a very limited space around the parent plants, but the density of seed is low since most seeds do not spontaneously fall from spikes. In contrast, many seeds are spread by combine harvesters. In this study the maximum dispersal exceeded 18 m from established stands in cereal fields, although the modal distance was close to the origin. In addition, the action of the combine harvesters tended to accumulate *L. rigidum* seeds predominantly under the straw swath, with some lateral movement. This action could explain the fine scale banded pattern of *L. rigidum* in cereal fields. Although the treatment of straw by the standard and straw chopper combines differed, the resultant seed distribution showed few differences.

1. Introduction

Many weeds exhibit an uneven distribution in fields, and sometimes patchiness may differ depending on the sampling scale (Rew *et al.*, 1997; Cousens & Croft, 2000; Rew & Cousens, 2001). The spatial distribution may be related to the interaction of numerous factors, such as soil type (Häusler & Nordmeyer, 1995; Dieleman *et al.*, 2000), cultivation (Marshall & Brain, 1999; Colbach *et al.*, 2000b), harvesting (Ballaré *et al.*, 1987b; McCanny & Cavers, 1988), herbicide efficacy (Dieleman *et al.*, 2000) and crop interference (Weiner *et al.*, 2001), all of which can affect seed distribution, germination and survival. In recent years, the uneven distribution of weeds has lead to the development of site-specific weed control (Gerhards *et al.*, 1997a; Paice *et al.*, 1998) within precision agriculture (Heisel *et al.*, 1997; Nordmeyer *et al.*, 1997), which optimises agricultural inputs (e.g. herbicides) by varying application rates to match within-field requirements. However, the effect of agricultural factors on seed distribution must be quantified to improve our predictions of weed populations.

Many studies have addressed the spread of weeds (McCanny & Cavers, 1988; Howard *et al.*, 1991; Rew & Cussans, 1997; Thill & Mallory-Smith, 1997; Woolcock & Cousens, 2000; Colbach & Sache, 2001; Wallinga *et al.*, 2002), since there is great interest in evaluating the dynamics of weed populations. Also, an improved knowledge and understanding of seed dispersal could be useful in terms of theoretical ecology, in order to explain the uneven distribution of weed populations within fields (Colbach *et al.*, 2000a). Mathematical modelling of seed dispersal and of movement by farm equipment has been used to explain the rates of spread of target weed species, and to suggest implications for weed management. For example, combine harvesting promotes the rapid spread of weeds (McCanny & Cavers, 1988), which causes the patches to extend over time. Combine harvesting has been analysed as a cause of dispersal within (Ballaré *et al.*, 1987b; McCanny & Cavers, 1988) and among fields (McCanny *et al.*, 1988), but has rarely been related to spatial variability of weed populations (Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a). Colbach *et al.* (2000b) pointed out that the spatial variability of populations along and across crop rows could be affected by combine harvesting, though the level of effect would depend on the crop stature and the weed habit. This could be especially true in cases in which weed spatial variability differs dramatically depending on the direction and the scale of analysis (Rew & Cousens, 2001).

Lolium rigidum Gaudin (annual ryegrass) is a common grass weed in cereal fields under Mediterranean climate (Monaghan, 1980; Recasens *et al.*, 1997); in Spain it is particularly abundant in the North-East, where it is the main weed in winter cereals. Little is known about the dispersal of this species. *L. rigidum* does not shed its seeds spontaneously before crop harvest, and even after harvest most seeds are dispersed as clustered spikelets or spike fragments (Recasens *et al.*, 1997), indicating that seeds seldom fall freely from spikelets without the help of a mechanical action. Moreover, even after combine harvesting a considerable proportion of seeds (16%) can still be attached to broken segments of seed heads (Gill, 1996a). *L. rigidum* could be controlled through seed management at harvest (Gill, 1996a, 1997), and some studies indicate that as much as 80% of total seed could be removed at harvest if the chaff fraction is collected and destroyed (Walsh, 1996; Gill, 1997; Walsh & Parker, 2002), but growing season of the crop and weed play a significant role in the proportion of *L. rigidum* seed that can be collected in any given year or field.

The dispersal action of combines on *L. rigidum* seed has not yet been quantified as it has been for other species like *Datura ferox* L. (Ballaré *et al.*, 1987b) and *Bromus* spp. (Howard *et al.*, 1991). The latter species differ in seed size and dispersal mechanisms to *L. rigidum*. The seeds of *Bromus* spp. are larger than those of *L. rigidum* and are shed freely when mature. *D. ferox* is a tall broad-leaved weed, whose seeds are large (*c*. 5 mm in diameter) and loosely disposed in large seed pods.

Here we studied the contribution of two types of combines, standard and those with an attached straw chopper, to *L. rigidum* dispersal parallel and perpendicular to the cutting swath. These two combining methods are the most common harvesting systems used in conventional cereal fields in north-east Spain. We evaluated the effect of these combines on the fine scale distribution pattern of *L. rigidum* seeds and the subsequent seedling patterns. In addition, we describe the fine scale variability of *L. rigidum* seedling populations and discuss this on the basis of the treatment of crop debris by combines.

2. Materials and methods

2.1. Dispersal of seeds by combine harvesters

Our experiment was performed in Concabella (Catalonia, north-east of Spain, 41º40’51” North 1º20’6” East), in a no-tillage winter barley (*Hordeum distichon* L. cv. Hispanic) crop with no natural infestation of *L. rigidum*. Field management is summarised in Table 1.

Table 1 Agronomy of the experiment in Concabella, Spain.

Weed sowing	*Lolium rigidum*	October 19, 2000	6000 seeds m^{-1}
Crop sowing	*Hordeum distichon* cv. Hispanic	October 19, 2000	200 kg ha^{-1}
Herbicide application	Chlorsulphuron + Isoproturon	January 10, 2001	15 g.a.i. ha^{-1} +1500 g.a.i. ha^{-1}
Fertilisation	Ammonium Nitrate	February 8, 2001	200 kg ha^{-1}
Crop harvest		June 7, 2001	

The experiment was a one factor design, the combine harvester, and three replicates. Three plots (80 m wide × 40 m long) were established 35 m apart (Fig. 1). Within each plot, two subplots (40 m wide × 40 m long) were delimited. One was harvested with a standard combine (Deutz Fahr 3575H) with a cutting width of 4.80 m, while the other was harvested with the same combine but with the straw chopping attachment connected to the outlet (these machines will be referred to herein as CC – standard combine, and SC –straw chopper combine, respectively). In both situations the chaff spreading mechanism was connected, since the field was under no-tillage regime.

Prior to crop seeding, a 4 m wide × 5 m long (along crop rows) stand/area, located in the centre of each subplot was sown with *L. rigidum* seed at approx. 6000 seeds $m^{-2,}$, on 19 October, 2000. The stands were covered with a plastic sheet during herbicide application to protect weed. Seed production at harvest in each stand was evaluated collecting six 25 cm × 25 cm quadrats randomly placed within the stand, immediately prior to crop harvest. These quadrats were used to evaluate seed production per unit area. Stand seed production at harvest was 55,260 ± 3985.4 seeds m^{-2}, which is quite high compared to seed production reported by Gill (1996b). On 7 June, 2001, all plots were harvested. The combine was driven at 6 km h^{-1} in the direction of crop rows.

The distance between plots and stands prevented seed overlap during dispersal. There was no to very low wind during crop harvest.

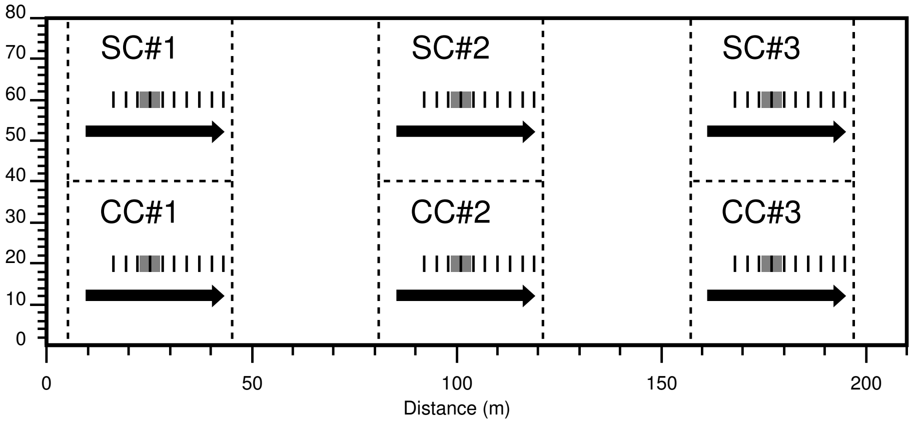

Fig. 1 Diagram depicting the experimental layout. The grey-shaded areas are the *L. rigidum* seeded stands/areas. The black arrows indicate the movement of the combine during harvesting. The black vertical bars indicate the positions of transects along the combine track. CC represents standard combine and SC represents straw chopper combine.

The sampling grid was designed to detect forward and backward seed movements (Fig. 1), and also to detect seed dispersal along the perpendicular axis (lateral seed movement). Thus, the strip opened by the harvester was sampled from 9 m behind the centre of the stand to 18 m in front of it (total length 27 m). Along this 27 m stretch 10 transects perpendicular to the track of the harvester were sampled (Fig. 2). The transects were 3 m apart. Five samples were taken in each transect: one centred on the swath and two more on each side, 1 m apart (Fig. 2). Each sample was composed of four subsamples, which were taken in a cross-shaped scheme, by vacuuming four areas of 10 cm × 10 cm which were placed within a 20 cm radius. To evaluate seed dispersal, only germinable seeds were counted. To achieve this samples were sorted from large straw pieces and small stones and were put into plastic trays and irrigated by sprinklers from 7 August to 20 December, 2001. Seedlings were counted weekly and the content of the trays was mixed to encourage further germination, this sequence was continued until further germination was very low when the experiment was terminated. Hereinafter we will refer to the seedlings recovered from the trays as seeds, to distinguish these results from the intensive survey of natural populations explained in the next section.

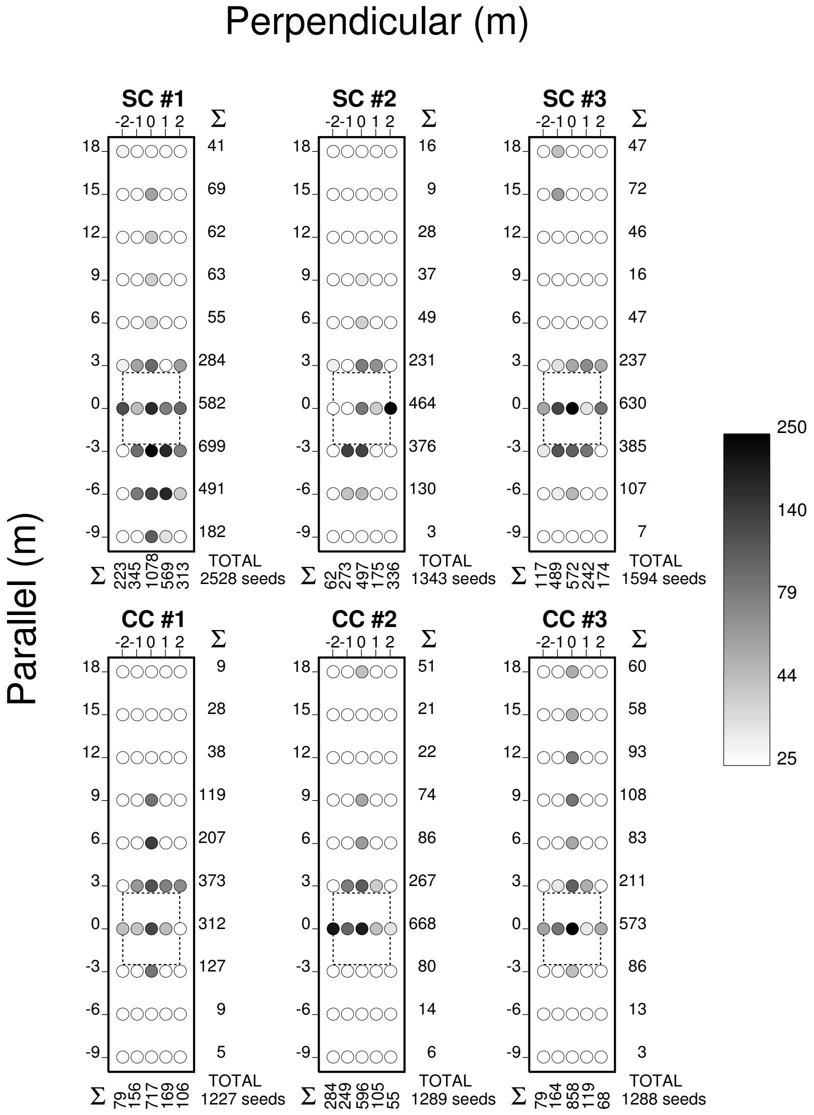

Fig. 2 Sampling design for each subplot. The inside rectangle (dashed line) indicates the position of the *L. rigidum* seeded stands/areas. The total number of seedlings recorded across each perpendicular transect is given on the right side of each plot; the numbers below each plot indicate the total number of seedlings recorded along the parallel transect lines. The total sum of seedlings recorded is given in the bottom right corner. The grey scale refers to the number of seedlings in each sample. CC represents standard combine and SC represents straw chopper combine.

2.2. Fine scale spatial variation of L. rigidum populations

In order to describe fine scale variation of *L. rigidum* populations an intensive survey was performed in another cereal field over a three year period. We selected four 10 m × 10 m field plots representing a wide range of ryegrass densities within a wheat field (*Triticum aestivum* cv. Soissons) conventionally harvested along crop rows, located in Calonge de Segarra (Catalonia, north-east of Spain, 41º45’32” North 1º31’29” East). Only one herbicide application was applied to the field during the survey (years 2002 and 2003). A mixture of herbicides (chlorsulfuron at 9 g.a.i. ha^{-1} plus tribenuron-methyl at 9.375 g.a.i. ha^{-1}) was applied to control dicotyledonous weeds on March 3rd 2002. These plots were surveyed in mid summer 2001, winter and mid summer 2002 and winter 2003 in order to establish straw position after harvest and to evaluate spatial distribution of seedlings in the following growing season for two consecutive years. Straw position after harvest was recorded as present or absent (binary data) on a regular 0.5 m × 0.5 m grid, and sampling points were aligned in an east to west direction, which was the orientation of the crop rows. *L. rigidum* seedlings were counted using 10 cm × 10 cm quadrats on the same regular grid. All measurements were performed for two consecutive years to assess the effects of straw deposition on the distribution of the seedlings and to evaluate year-to-year variation in spatial distribution.

2.3. Statistical analysis

2.3.1. Dispersal of L. rigidum *seeds by combine harvesters*

A preliminary analysis of data indicated that seeds were dispersed according to a maximum near the point of introduction, with short tails backward and long tails forward. According to Howard *et al.* (1991), this pattern of redistribution can be described by a compound model, formed by a normal function centred slightly behind the point of introduction, and a negative exponential function from the point of introduction forwards. It is explained as the conjunction of two distinct phenomena: most seeds (in a p proportion) are released shortly after being collected, but the transit of seeds inside the combine is faster than its movement across the field, which results in the slightly backward displacement of seeds. Long forward tails are explained because remnant seeds (a $(1-p)$ proportion) are released much more slowly and gradually while are being processed by the combine. To avoid differences between plots caused by differences in the total number of seeds recorded, all analyses were performed on the proportion of seeds collected at a given position (transect) for a plot.

The shape of seed distribution was approximately the same in all perpendicular transects, so all transects were described jointly. Lateral movement of seed dispersal was described by a Cauchy distribution function because the ends of the transects (outer values) were too high to be adequately described by a normal one. It is noteworthy that the Cauchy distribution function has some peculiar properties: it does not obey the central limit theory and the mean and standard deviation of the Cauchy distribution function are undefined. However, these reasons do not make it an inappropriate model for dispersal (Shaw, 1994). The model fitting was performed on the number of seeds recovered at each point, divided by the total number of seeds collected at a given distance (transect). Therefore at each distance sampled the seeds recovered summed to one and thus had the same weight when adjusting the function, independently of distance to focus and the total number of seeds.

Functions were fitted with the non-linear regression procedure –PROC NLIN of SAS (1999)– and treatments were compared using the indicator variable approach (Neter *et al.*, 1990; Juliano, 1993). The indicator variable approach has the advantage that it produces an explicit test of the null hypothesis of equal parameters (Neter *et al.*, 1990).

The resulting equations fitted to the longitudinal movement are as follow:

if distance < 2.5 m:

$$Normal(\mu,\sigma) = (p + dp \cdot combine)\left[\frac{\exp\left(-\frac{(distance - (\mu + d\mu \cdot combine))^2}{2(\sigma + d\sigma \cdot combine)^2}\right)}{(\sigma + d\sigma \cdot combine)(2\pi)^{0.5}}\right]$$

if distance ≥ 2.5 m:

$$Normal\,(\mu,\sigma) + Exponential\,(\beta) = (p + dp \cdot combine)\left[\frac{\exp\left(-\frac{(distance - (\mu + d\mu \cdot combine))^2}{2(\sigma + d\sigma \cdot combine)^2}\right)}{(\sigma + d\sigma \cdot combine)(2\pi)^{0.5}}\right]$$
$$+ (1 - (p + dp \cdot combine))\left[\frac{1}{(\beta + d\beta \cdot combine)}\exp\left(-\frac{distance}{\beta + d\beta \cdot combine}\right)\right]$$

where p is the proportion of seeds dispersed according to the normal function, dp is the difference in that proportion between combines, σ is the scale parameter of the normal function, $d\sigma$ is the difference in scale parameter between combines, μ is the position parameter of the normal function and $d\mu$ is the difference in position between combines, and β is the shape parameter of the exponential and $d\beta$ is the difference in shape between combines. The variable *combine* takes values 0 or 1 arbitrarily assigned to the SC and the CC, and is included to account for the difference between treatments. The parameters $d\mu$, $d\sigma$ and $d\beta$ estimate the differences between combines in the values of the parameters μ, σ and β respectively. If the parameter estimates are significantly different from 0, then the two combines differ significantly in the corresponding parameters. In that case, for the SC, the estimates of the parameters μ, σ and β are the estimates of the treatment parameters μ_{SC}, σ_{SC} and β_{SC}. For the CC, $\mu+d\mu$, $\sigma+d\sigma$ and $\beta+d\beta$ are the estimates of the treatment parameters μ_{CC}, σ_{CC} and β_{CC}. The cut-off point between function domains was established at 2.5 m since it is the limit of the weed seeded stand.

The lateral seed movements were described using the following equation:

$$Cauchy = \frac{1}{(s + ds \cdot combine) \cdot \pi \cdot \left(1 + \left(\frac{distance}{(s + ds \cdot combine)}\right)^2\right)}$$

where s is the shape parameter of the Cauchy distribution function and ds is the difference between combines. This equation does not include any position parameter because the seed movement is assumed to be symmetrical and centred on the swath. The interpretation of parameters is the same as for the previous equations.

2.3.2. Fine scale spatial variation of L. rigidum *populations*

The spatial structure of populations and straw patches was studied by means of the analysis of indicator semivariance (Isaaks & Srivastava, 1989; Goovaerts, 1994a; Deutsch & Journel, 1998) in space, simultaneously with examination of spatial distribution maps. Mapping is a necessary complement to structure function analysis since the shape of the functions may not correspond unambiguously to a single type of structure (Legendre, 1993). The indicator semivariance was used since straw presence is already a binary (indicator) variable, and weed density can be readily converted into an indicator variable through coding in relation to a cut-off. Above the threshold the original variable is coded as 1, and below it the weed density is coded as 0. The spatial relationship between straw presence and weed density, and the relationship of these two variables between two consecutive years was analysed by a cross-semivariogram. This analysis was used to describe the extent of spatial relation between variables (Isaaks & Srivastava, 1989; Goovaerts, 1994a). In such a way, the cross-semivariance indicates the association between straw presence and high weed density.

Only three plots from the original four were used in the analysis because one was located too near to the field margin and thus the combine passed through it twice. This double pass made it difficult to interpret results, since straw swaths did not correspond to their original position and *L. rigidum* seeds were probably deposited twice. Since the remaining plots did not differ noticeably in the direction of straw swaths, they were pooled for analysis.

The analysis of auto and cross-semivariance was carried out by calculating and plotting semivariograms in two perpendicular directions, parallel and perpendicular to crop rows. The shape of the semivariograms allowed us to describe the spatial pattern of the patches (Legendre & Fortin, 1989). Semivariograms were calculated using the GSLib subroutine, GAMV (Deutsch & Journel, 1998), for straw presence and weed density. These analyses were performed for the three areas selected and two growing seasons (2001-2002 and 2002-2003).

3. Results

3.1. Dispersal of L. rigidum seeds by combine harvesters

The number of seeds collected from the two types of combines did not differ significantly (Student’s *t*-test = 1.53, *P* = 0.2649), although one replicate for the SC had almost twice as many seeds as the replicate that showed the minimum (Fig. 2). The seeds of *L. rigidum* were deposited in a similar manner by the SC and CC, with the maximum density near the centre of the stand and a long redistribution in front of it (Table 2 and Fig. 3). The mean distance (± SE) of seed dispersal (calculated as the distance weighed by the amount of seeds at a given distance) was 0.084 ± 0.727 m for the SC and 3.130 ± 0.474 m for the CC.

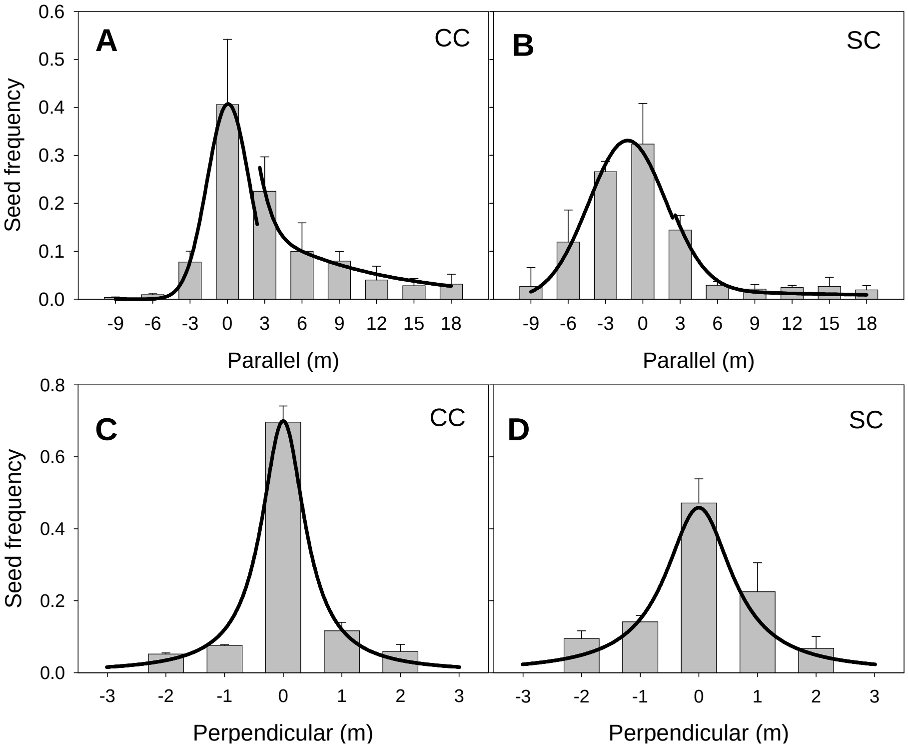

Fig. 3 Effect of combines on *Lolium rigidum* seed dispersal parallel (A, B) and perpendicular (C, D) to swaths. CC represents standard combine and SC represents straw chopper combine. Boxes are mean seed frequency (± SD) for the three replicates and the solid lines are the fitted functions.

Table 2 Comparison of the total number of seeds captured and the proportion of *L. rigidum* seeds remaining in the seeded stand/area, and recovered behind and in front of it. CC represents standard combine and SC represents straw chopper combine. Values in parentheses are standard errors.

	SC	**CC**	**Difference**	***P*-value**	**Confidence interval 95% for difference**	
Captured seeds	1821.7 (360.52)	1268.0 (20.50)	553.7	0.2649	-448.9	1556.3
Proportion in front	0.265 (0.0194)	0.504 (0.0669)	-0.239	0.0265	-0.432	-0.046
Proportion behind	0.412 (0.0683)	0.091 (0.0122)	0.321	0.0098	0.129	0.514
Proportion on the focus	0.324 (0.0489)	0.406 (0.0787)	-0.082	0.4252	-0.339	0.175

The fraction of seeds recovered behind and in front of the stand differed significantly between combines (Table 2), and it was also stated by the values of the *p* parameter (Table 3), indicating the proportion of seeds that were not moved further from the focus. The seed dispersal pattern behind the limits of the source differed between combines, as stated by the estimates of the normal function parameters (Table 3). The position parameter μ, indicating the location of maximum seed density, was placed 0.0588 m in front of the focus for the CC, whilst it was -1.2265 m behind it for the SC. Also the value for the parameter σ, indicating dispersion of the seeds around the maximum, was statistically different between combines (Table 3). The value of the parameter σ_{CC} was 0.5682 and the value of σ_{SC} was 1.0449, indicating that the distribution of seeds by the SC was less concentrated.

Table 3 Estimates of the parameters (with their standard error) of the function fitted to the parallel and perpendicular seed movements, with the difference between combines and the significance of such differences.

		Parameter estimate (SE)		**Difference**	**P-value**	**Confidence interval 95% for difference**	
		SC	**CC**				
Parallel	μ	-1.227 (0.2551)	0.059 (0.03351)	1.285	0.0036	0.440	2.130
	σ	1.045 (0.0885)	0.568 (0.0574)	-0.482	0.0001	-0.713	-0.250
	p	0.867 (0.0588)	0.575 (0.0596)	-0.292	0.0015	-0.466	-0.118
	β	7.445 (7.5706)	3.124 (0.8140)	-4.342	0.6266	-22.142	13.458
Perpendicular	s	0.694 (0.0581)	0.455 (0.0251)	-0.239	0.0004	-0.369	-0.110

μ and σ parameters are the normal function parameters, *p* is the proportion of seeds dispersed by the normal function. β parameter is the shape parameter of the exponential decline. *s* is the shape parameter of the Cauchy function fitted to the perpendicular distribution of seeds. CC represents standard combine and SC represents straw chopper combine.

While the above analysis shows a short dispersal distance for more than the 50% of the seeds, a significant proportion were moved greater distances and this is of considerable importance in the context of the expansion of patches. Although the proportion of seeds carried forward by both combines was different, the estimates of the parameter β, which describes the decline in seed density in front of the point of introduction, did not differ significantly between combines (Table 3). The lack of statistical differences may be related to the poor estimation of the forward tail and the lack of samples at extreme distances. The maximum dispersal distance was not assessed for either combine, since in all replicates some seeds were found at the maximum distance sampled (Fig. 2).

With respect to the lateral movement of seeds, they were not homogeneously distributed across the swath opened by the combines. The dispersal in the direction perpendicular to the combine movement was limited and independent of dispersal parallel to the movement. For both SC and CC there was a clear accumulation over the central line, which corresponded to the central straw deposition in the case of the CC (Fig. 3). Differences between the central line and the margins ranged from 5 to 13 fold for the SC and CC, respectively. The latter concentrates the debris on a narrower band. Thus, the proportion of seeds on the central line was 69.62 ± 4.49% for CC and 47.16 ± 6.69% for SC (Student's *t*-test = -2.784, $P = 0.050$). The distribution of seeds was flatter and with more seeds dispersed away from the centre in the plots harvested by the SC, as shown by the value of the *s* parameter of the Cauchy distribution (s_{SC} 0.694 vs. s_{CC} 0.455).

3.2. Fine scale variation of populations

The measurements recorded in the experimental field in Calonge de Segarra were first explored by mapping. Data points were plotted with their actual values. Straw deposition and seedling density maps for one of the three plots selected are shown in Fig. 4. The other two plots are so similar that maps are not shown. The percentage of straw covering the surveyed surface ranged from 24.04 to 44.22% (average 31.2% in 2001 and 37.8% in 2002). Mean *L. rigidum* seedling density within each plot ranged from 1026.08 to 2232.88 seedlings m^{-2}, and the overall average *L. rigidum* density was 1564.47 seedlings m^{-2} in 2002 and 1910.43 seedlings m^{-2} in 2003.

Straw presence and *L. rigidum* seedling density were autocorrelated in both directions and for both years, indicating that the scale at which spatial structure occurred was greater than the distance between two neighbouring quadrats (Fig. 5A, 5B, 5C, 5D). The auto-semivariograms of straw presence (Fig. 5A, 5B) and seedling density (Fig. 5C, 5D) showed a similar pattern in both years. Furthermore, the cross-semivariograms also showed a similar pattern, indicating that these two variables have a shared spatial structure (Fig. 5E, 5F), and are positive, indicating a positive relationship between straw presence and high weed density. The extremely low cross-semivariance values between straw and weed density parallel to swathes in 2002 (Fig. 5F) suggest a strong association between straw and high weed density.

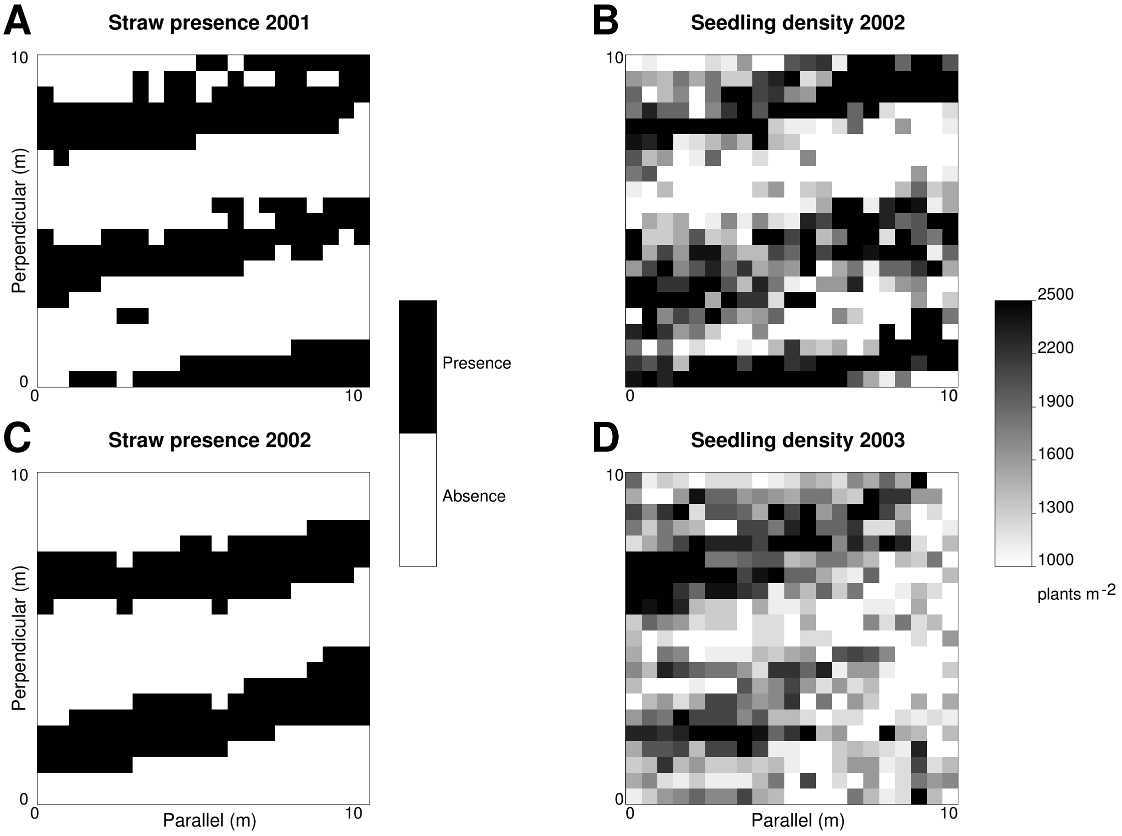

Fig. 4 Maps of straw deposition (A, C) and seedling density (B, D) in the following growing season. The black areas in straw maps denote zones that were occupied by straw and chaff after harvest, whilst white areas are straw free. Scale in seedling density maps is expressed in plants m^{-2}. The plot shown is 10 m × 10 m.

Spatial semivariance coefficients increased at a greater rate across than along crop rows. There was a clear sinusoidal pattern in the direction perpendicular to crop rows and to the combine movement across the field. Two peaks were observed for all variables, the first at about 2 metres, and the second at about 6 m from the origin, except for seedlings in 2002, that present an irregular pattern further of the 4 m (Fig. 5C). Semivariance coefficients increased with distance up to 2 m in 2001 and up to 2.5 m in 2002, corresponding to the difference in straw presence and weed density between the focal points and distances from these points.

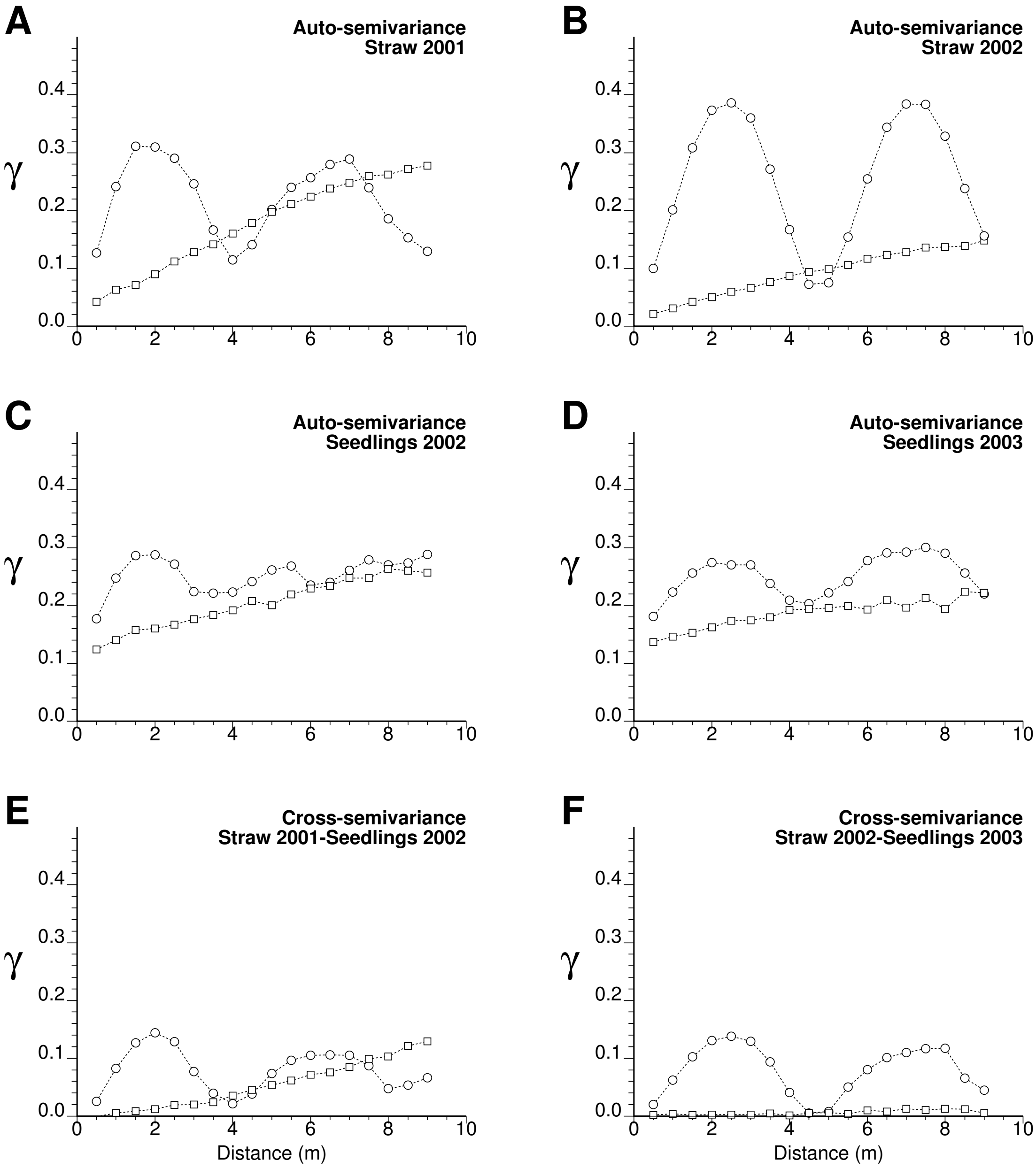

Fig. 5 Auto-semivariograms of straw presence (A, B) and seedling density (C, D), and cross-semivariograms between straw presence and seedling density (E, F). γ is the spatial semivariance coefficient. Squares (□) indicate the direction parallel to crop rows; circles (○) denote the direction perpendicular to crop rows.

The auto-semivariogram of straw presence and seedling density along crop rows followed a clear monotonic increasing pattern because of loss of auto- and cross-correlation with distance. The increase of semivariance is explained by the fact that straw swaths were not aligned with the sampling grid (Fig. 4A, 4C); if this had been the case, the auto-semivariogram would have been 0 in that direction for all distances analysed. The semivariance values for *L. rigidum* seedlings were higher at short distances than those for straw presence, since density values were much more variable than those of straw, which are restricted to presence or absence.

The cross-semivariogram of weed density between years (2002 and 2003) is shown in Fig. 6A. The low and not clearly patterned values of semivariance at all distances indicate a poor correlation between years. The cross-semivariogram of straw presence in 2001 and 2002 (Fig. 6B) shows an inverted pattern with respect to straw auto-semivariograms (Fig. 5A, 5B). The cross-semivariogram of straw presence perpendicular to rows presents negative values in the beginning, indicating that straw lines are intercalated, and descends to a local minimum at 2.5 m, which reflects the distance between straw lines of the two consecutive years.

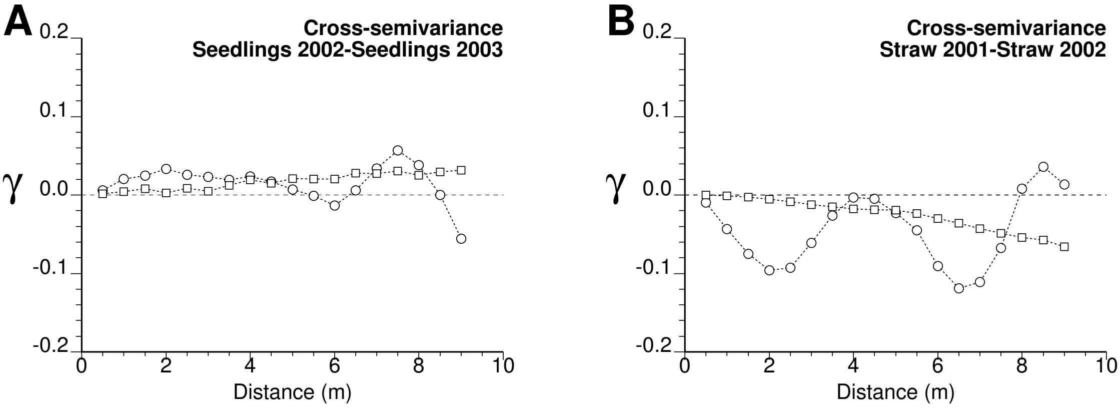

Fig. 6 Cross-semivariogram of seedling densities (A) and of straw presence (B) in two consecutive years. γ is the spatial semivariance coefficient. Squares (□) indicate the direction parallel to crop rows; circles (○) denote the direction perpendicular to crop rows.

4. Discussion

4.1. Dispersal by combines

Secondary dispersal of *L. rigidum* seeds was assessed in an experiment that simulated agricultural conditions in which the weed is common. In these conditions, combines make a significant contribution to seed dispersal while primary dispersal might be less relevant. As pointed out Walsh & Parker (2002), a high proportion of *L. rigidum* seeds, ranging from 46 to 71%, remain on spikes at harvest time depending on crop and season, thus entering the header of combines during harvesting. The remaining seeds are assumed to fall freely from spikelets, but the percentage can vary as a function of the harvest time. A preliminary analysis (results not shown) suggested that a 6.44% of the seeds could had been dispersed by the harvest time. Since it was not actually sampled, it was not used in the following analyses. This pool of pre-harvest dispersed seeds are likely to be displaced short distances. A large proportion of *Alopecurus myosuroides* Huds. seeds (Colbach & Sache, 2001), a species with slightly smaller seeds than those of *L. rigidum*, are dispersed in the immediate neighbourhood of their mother-plant, mainly because of gravity-related dispersal, and very few seeds are collected further than 4 m. The majority of *Bromus sterilis* L. (99%) and *Anthriscus sylvestris* (L.) Hoffm. (87%) seed marked in a field margin, and 84.5% of *B. sterilis* seeds marked in an open field are disseminated within 1 m of the source (Rew *et al.*, 1996b). In fact, for many weeds natural dissemination distances are well below 4 m (Pacala & Silander, 1990; Howard *et al.*, 1991; González-Andújar & Perry, 1995) and seeds remain within the focal point (Ballaré *et al.*, 1987b). Short dispersal distances in annual weeds is not disadvantageous as the mother-plant will die and leave an empty space; however, it could be a drawback if the seed production of adult plants is negatively influenced by overcrowding (Ballaré *et al.*, 1987b). In addition, primary dispersal (and its importance in relation to secondary dispersal) will affect the abundance and pattern of patches. Unfortunately, this issue is outside the scope of our work, but might be relevant to develop further research on dispersal and patch expansion.

Our results show that the dissemination of *L. rigidum* seeds is strongly influenced by the action of combine harvesters. These machines have the potential to move seeds over a great distance, presumably more than 18 m for *L. rigidum*, in the direction of combine movement, a finding which is consistent with many species such as *Panicum miliaceum* L. (McCanny & Cavers, 1988), *Bromus* spp. (Howard *et al.*, 1991; Rew *et al.*, 1996b), and *Datura ferox* (Ballaré *et al.*, 1987b).

Although in some studies backward dispersal was not sampled (Ballaré *et al.*, 1987b), there were results from other studies (Rew *et al.*, 1996b) indicating that backwards seed movement occurs during harvesting. Combines also disperse *L. rigidum* seeds backwards; this movement may occur because of the lower speed of combine movement (forward) than that of straw debris (backward) within the combine, which would result in an overall backwards movement of debris. However, it may also be the result of the propulsion of the straw by the straw chopper. These effects have been described as a short range movement (Howard *et al.*, 1991), but they have only rarely been documented for other weeds. Nevertheless, backward and forward movements are not relevant to the positional stability of weed patches, since the (weighted) mean distance that the seeds were moved was close to zero. Therefore, we assume that weed patches (or at least the foci or higher density zones) do not move as the result of harvester action. However, it is pertinent to consider the movement of a few seeds that are swept forward by combines. This long distance might cause the appearance of new foci (Shaw, 1995; Wallinga *et al.*, 2002) and remnant seeds inside the combine can infest new fields (McCanny & Cavers, 1988). It should be noted that the importance of such movement, and the risk of yield loss at distances further from the original foci, is dependent on the quantity of seeds that are swept away which, in turn, is dependent on the relative importance of secondary versus primary dispersal.

Some modelling studies (Le Corre *et al.*, 1997; Colbach & Sache, 2001) have described seed dispersal as a single Weibull function or a conjunction of two continuous functions, indicating that at least two mechanisms contribute to the dispersal. The description of seed dispersal of *L. rigidum* over all distances with a single function or a conjunction of two continuous functions was not possible. However, the set of two functions that provided two separate descriptions of the dispersal in front and behind the focus allowed us to illustrate the differences between the combines and discuss their effect on seed dispersal.

Although the normal function explains most of the seed movement, it is the least important when studying dispersal because the movement of seeds predicted by this function is scarce, and it provides poor information on relevant subjects such as the risk of infestation of new zones and the expansion of patches. Nevertheless the exponential function fitted to the forward movement offers valuable information. This is a main factor that should be considered when analysing the risk of expanding patches. Therefore, the probability of seeds reaching longer distances is greater for the CC, although there were no significant differences between the proportions of seeds recovered at the extreme distances sampled (statistics not shown, *P*-value = 0. 427).

According to Wallinga *et al.* (2002), a plant population can display a spread-out pattern if the forward tail of the projected seed dispersal curve declines more slowly than exponential. Therefore, in SC and CC, a closed front that moves forward at a constant rate is expected from year-to-year. Here we cannot determine whether the curves are exponential or power lines, although this assumption can be somewhat arbitrary (cf. Wallinga *et al.*, 2002). Moreover, the practical consequences of the kind of decline are still to be explored.

Our results show that the lateral seed aggregation is more relevant than longitudinal dispersal in the generation of patterns of seedlings. The accumulation of seeds under the central line by the action of both combines produced a fine scale pattern, characterised by high and low density zones which were separated by few metres (about 2 m but this depends on combine width). Differences in the perpendicular movement of seeds between combines were related to the straw treatment. Since both combines had the chaff spreading system connected to the outlet, the differences are related to an important fraction of seeds that are processed with the straw not with the fine chaff fraction. However, in relation to the risk of spreading weeds to new areas, the longitudinal movement is the most worrisome to farmers and weed scientists.

4.2. Fine scale variation of populations

The most consistent observation of the seedling spatial distribution is the repeated banded pattern every 4 m. As in many other studies, auto-semivariance increased much more steeply perpendicular to harvest lines than parallel to them. This is the pattern expected for any field in which weed patches are elongated in the direction of combine movement.

The most striking observation of the semivariogram is that the pattern is roughly the same as that reported by Dieleman and Mortensen (1999) for *Abutilon theophrasti* Medik. in corn (*Zea mays* L.) fields, despite differences in the latter crop-weed system. There are two substantial differences between our results and those of other studies that report similar spatial structures (Johnson *et al.*, 1996; Dieleman & Mortensen, 1999;

Colbach *et al.*, 2000a; Wiles & Schweizer, 2002). The first is the scale of the phenomenon. In our case the distance between the first peak and the first trough was about 2 m, whilst for other studies it falls over 10 m. The second difference is the periodicity of the pattern, which depends on the repeated passes of combines.

The elongated patch pattern of other weeds might depend on the cultivator action and ridge-tillage planters, which are not used in cereal fields in north-eastern Spain. Other factors, such as poor overlap of sprayer boom or of cultivation passes could lead to elongated weed patches (Dieleman & Mortensen, 1999); however, these are exceptions rather than the rule, contrary to our case where elongated bands of seedlings conformed the general pattern of the field.

Analysis of weed pattern stability through the cross-semivariogram between the 2002 and the 2003 density revealed, on this fine scale, a lack of a stable relationship between years. In contrast, other authors (Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a) who found large-scale patch stability related to the presence of a persistent seed bank and to the restricted action of combines and other farm machinery because most of the weed seed was not retained on the adult plants. In our study the main seed movements were caused by combine harvesting. Although some movement could result from the planter and chisel ploughing, these are unimportant contributions since we observed very good agreement between straw position after harvesting and high-density zones of weed in the following growing season. If ploughing or sowing had a greater impact, the banded pattern would probably be absent. Similarly, if natural dissemination played a key role in seed dispersal, it would have been detected in the spatial pattern as a positive association between weed density over years because of the short distance dispersal of *L. rigidum* seeds. The role of seed banks from previous years should be discarded because of the short life of seeds in the soil (Gill, 1996a); some authors (Gramshaw & Stern, 1977; Gill, 1996a) have reported seed bank decay in one year ranging from 75% to 90%. Thus even in the presence of a high seed bank (in our case between 2000 and 6000 seeds m^{-2}, unpubl. obs.) mainly the seeds produced in the immediately preceding cropping season should be considered.

Non-spatial models of population dynamics use averages as parameters, and model outputs are given as mean densities (van Groenendael, 1988). However, studies that rely on mean densities do not provide a precise description of weed population distribution or spatial dynamics in fields (Wallinga, 1995; Paice *et al.*, 1998; Dieleman & Mortensen, 1999). In this case, the short distance variation displayed by *L. rigidum* seedlings can hinder the application of theoretical models under field conditions. Moreover, spatial structure analysis might be flawed because of inadequate scales of analysis. So, if the aims of spatial structure description are focused on estimation of weed density at unsampled locations (e.g. kriging, which has become one of the most popular methods), the results could be absolutely wrong. This fine scale variation can make it difficult to determine the overall density of any given location and the effects on yields might be even harder to assess.

It is reasonable to affirm that practices like chaff collection might be useful to control this weed, as this agricultural practice can account for a large fraction of the seeds dispersed. Moreover, chaff collection could prevent the appearance of zones with a high density of weeds which can ensure patch survivorship (Dieleman *et al.*, 1999).

This research indicates that *L. rigidum* seed dispersal is strongly affected by combines, which have a great potential to move seeds great distances, and concentrate seeds on a narrow strip. Our results also show that seed dispersal by combines is a major factor contributing to the patchiness of *L. rigidum*. Improvements in weed control could be achieved by modifying tactics of seed management, especially with respect to management of harvest residues, thus reducing the dispersal of seed into new areas.

CHAPTER V

MODELLING THE SPATIAL DYNAMICS OF *LOLIUM RIGIDUM* IN CEREAL FIELDS

Summary

Seed dispersal is included in a demographic model in order to assess the population dynamics and the spread of *Lolium rigidum* from a point source. The model is used to describe the behaviour of *L. rigidum* populations in the absence of control practices and to predict the effect of various control strategies. The sensitivity of the model to variation in demographic parameters is generally low, except for seed production, for which, within the range of natural variation, sensitivity can be up to 99%. Spread rate is hardly affected by changes in demographic parameters, except for fecundity, which at its lowest limit keeps the population at a critical size and leads to occasional extinction. Thus, the management practices with the greatest influence on population growth would be those affecting seed production or seed losses during dispersal. Factors most affecting patch spread would be weed phenology (mainly rate of spontaneous seed shed at harvest) and disruption of the cereal cycle (fallow), but not demographic parameters, since these do not affect dispersal distance. The contribution of dispersal to spatial patterning is discussed.

1. Introduction

Studies of the spatial distribution of plants have gained increasing attention in plant ecology, including weed science. The incorporation of space to population dynamics models greatly increases their realism because spatial models preserve the position of individuals and the movement of propagules is allowed between locations (van Groenendael, 1988). Furthermore, studies that rely on mean densities cannot provide a description of the spatial dynamics of weed populations (Silvertown *et al.*, 1992; Wallinga, 1995; Paice *et al.*, 1998; Dieleman & Mortensen, 1999). Theoretical models have been used to predict the rates of spread and the effect of patchiness on the population dynamics of weeds (Perry & González-Andújar, 1993; Wallinga, 1995; Woolcock & Cousens, 2000). However, few attempts have been made to deal with specific weed cases (Ballaré *et al.*, 1987a; González-Andújar & Perry, 1995), since a great deal of information must be known before specific weed dynamics can be modelled accurately.

An important factor affecting the spatial structure of weed populations is seed dispersal. Mathematical models have been used to give *post hoc* explanations of population spread and to define the implications of dispersal for the control of expanding populations. The rate and pattern of spread is influenced by the shape of the seed dispersal curve around the parent plant, which in turn might be affected by both biotic and abiotic factors (McCanny & Cavers, 1988; Howard *et al.*, 1991; Rew & Cussans, 1997). Such dispersal curves are often described by negative exponential or negative power law functions (Portnoy & Willson, 1993). However, the dispersal curves in the case of dispersal by harvest machinery are fit to complex functions (Howard *et al.*, 1991; Blanco-Moreno *et al.*, 2004) since dispersal may occur in more than one dimension, and not necessarily at the same rates. Moreover, different kinds of implements can exert different effect on seed dispersal (Rew & Cussans, 1997).

Beside dispersal there are many other factors affecting the rate of growth and expansion of populations. Density-dependence has been shown to be a rather general rule for many organisms (Hassell, 1975; Watkinson, 1980; Coomes *et al.*, 2002) which acts at different life cycle stages. For plants, density dependence has been found at recruitment (Lintell Smith *et al.*, 1999), at survival to maturity (González-Andújar & Fernández-Quintanilla, 1991), at *per capita* growth (Watkinson, 1980; Lintell Smith *et al.*, 1999), and at seed production (Watkinson, 1980; Perry & González-Andújar, 1993). The density-dependent population regulatory mechanisms keep the population at an equilibrium density. This equilibrium depends on the competitive ability of the species, the carrying capacity of the environment and their interaction with the management factors (e.g. herbicide application, tillage, combine harvesters, ...).

The inherent stochastic behaviour of demographic and dispersal processes is another important factor that can have a decisive role on the growth rate and spread of populations, particularly at low densities. Population dynamics models that include stochasticity in demographic and dispersal processes produce equiprobable discrete solutions instead of continuous and homogeneous ones. Such stochasticity in simulation models reduces the mechanistic behaviour and allows for different outcomes from identical initial conditions (Perry, 1988; Perry & González-Andújar, 1993). Stochasticity is more important at low population densities than at high densities, because at low densities there is a risk of extinction related to mortality and migration rates (Perry & González-Andújar, 1993).

In this paper we address the effect of dispersal, density dependence and stochasticity on the population dynamics of *Lolium rigidum* Gaudin (annual ryegrass), an annual weed with a non-persistent seed bank, through the simulation of the population evolution and dispersal from an initial introduction focus. *L. rigidum* is a very frequent cereal weed in the North-Eastern Iberian Peninsula and other Mediterranean climate areas. *L. rigidum* has been studied in terms of dispersal (Walsh & Parker, 2002; Blanco-Moreno *et al.*, 2004), competition (Gill, 1996a; Cousens & Mokhtari, 1998; González Ponce, 1998; Lemerle *et al.*, 2001; Izquierdo *et al.*, 2003), management of resistance (Burnet *et al.*, 1994; Gill *et al.*, 1996; De Prado *et al.*, 1997; Monjardino *et al.*, 2003; Neve *et al.*, 2003) and population biology (Gill *et al.*, 1996; Fernández-Quintanilla *et al.*, 2000; González-Andújar & Fernández-Quintanilla, 2004), since it is a serious weed in cereal crops world wide, and moreover it has developed resistance to several herbicide action groups (Burnet *et al.*, 1994; Heap, 1997; Llewellyn & Powles, 2001).

González-Andújar and Fernández-Quintanilla (2004) have recently published a simulation model using previously reported data to analyse the effect of various management practices on *L. rigidum* population size. However, their model failed to allow for any stochastic phenomenon and is adimensional. Our aim is to explore the effects of dispersal and management practices within an homogeneous landscape on the population dynamics and spatial structure of *L. rigidum*. The non-spatial population dynamics models raise several questions related to the dynamics of *L. rigidum* populations: 1) do non-spatial population models offer a reliable measure of *L. rigidum* dynamics? 2) which is the rate of spread of *L. rigidum* within a field? Does it depend on management? 3) which implications does management have for *L. rigidum* population spatial structure?

2. The model structure

The spatial population dynamics model used is based upon the life cycle model described by González-Andújar and Fernández-Quintanilla (2004) for non-spatial dynamics of *L. rigidum* (Fig. 1). This model will be referred to hereafter as the non-spatial model. However some modifications have been introduced, changing some control measures related to seed losses, and incorporating stochastic demographic and dispersal processes. All simulations were carried out in a 50.5 m × 50.5 m square and homogeneous field, divided in 0.5 m × 0.5 m pixels, totalling 10201 pixels. Although dispersal was simulated for individual seeds (see below), weed plants were summed in each pixel. Some neighbourhood simulation models retain the information of the spatial coordinates of every individual (Pacala & Silander, 1985), but these models yield outputs that are difficult to understand intuitively. Furthermore, the aggregation of individuals may have little effect on the output of the spatial population dynamics model since only a relatively small proportion of the variation in individual plant yield is accounted for by measures of local crowding (Firbank & Watkinson, 1987).

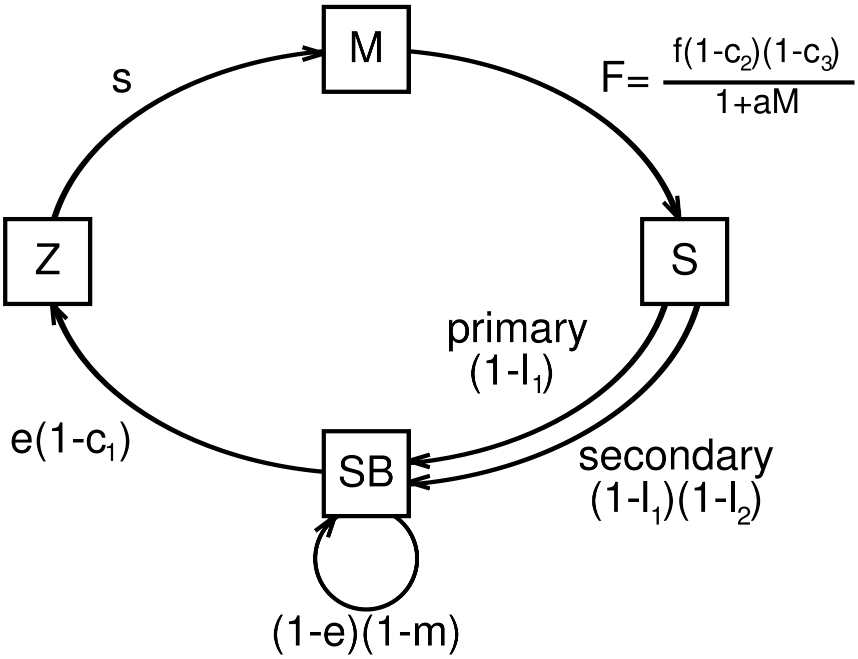

Fig. 1 Simplified life cycle of *L. rigidum*. Symbols are as follows: *SB*, seed bank; *Z*, seedlings; *M*, mature plants; *F*, fecundity per plant; *S*, Seed production; *e*, emergence; *s*, seedling survival to maturity; c_1 is control by delayed seeding; *f* is seed production per plant as density approaches zero, *a* is a parameter related to the strength of density-dependence; c_2 is control by herbicides and c_3 is control by competitive crops; l_1 represents seed losses owing to predation and conventional harvesting, and l_2, seed losses caused by seed catching at harvest.

2.1. Seedling emergence, seedling survival, fecundity and seed production

The number of seedlings emerging in the year *t* (Z_t, in seedlings pixel^{-1}) is given by the expression:

$$Z_t = e\,SB_t \tag{1}$$

where *e* is the proportional seedling emergence from the seed bank (SB_t, seeds pixel^{-1}) in the top 5 cm of soil. The seed bank is considered homogeneous in the upper 5 cm of the soil with only one pool of seeds with the same emergence pattern, because *L. rigidum* has a very low capacity to germinate from lower depths, and there is a very low persistence of seeds –less than 15% (Gill, 1996a; Taberner, 1996; Gill & Holmes, 1997)– in the soil after the first year. Also only one cohort of seedlings is considered in our model, although population structure with several cohorts has been documented elsewhere (Monjardino *et al.*, 2003; Pannell *et al.*, 2004).

However, some weed management practices as the delayed seeding can reduce the number of recruits through the destruction of part of the emerged seedlings. Although the removal rate depends on the emergence rate which is a function of thermal time and the moment of seedbed preparation (Forcella, 1998; Steadman *et al.*, 2003b), the level of control achieved by the delayed seeding is considered to be constant (González-Andújar & Fernández-Quintanilla, 2004). Thus, if c_1 represents the fraction of ryegrass seedlings destroyed by these practices, the number of seedlings at the beginning of the season is given by the expression:

$$Z_t = (1 - c_1) e\, SB_t\,. \qquad (2)$$

Although for many plants there is a density dependent relationship between seedling and adult plants, only some authors indicate such a relationship for *L. rigidum* (Monjardino *et al.*, 2003; Pannell *et al.*, 2004). They indicate a 2% mortality for densities above 5000 seedlings m^{-2} with no specific reference to experimental results, so this figure was not used in our simulations. Therefore, seedling survivorship to mature plants (M_t, mature plants pixel^{-1}) was considered a fixed proportion of all emerged seedlings:

$$M_t = s\, Z_t \qquad (3)$$

where *s* is the rate of the seedling survivorship.

Fecundity (*F*, seeds plant^{-1}) shows a density-dependent relationship with the number of mature plants, following a hyperbolic model (Watkinson, 1980):

$$F = f / (1 + a M_t) \qquad (4)$$

where *f* is the maximum number of seeds produced by an individual and *a* is a parameter related to the strength of density-dependence. Despite the values of the hyperbolic model parameters may vary widely, we used *f* = 935 and *a* = 0.34, the same parameter values given by González-Andújar and Fernández-Quintanilla (2004) to allow for straightforward comparisons between the non-spatial and the spatial models. However, seed production of *L. rigidum* survivors may be reduced by sublethal effect of herbicides (Monjardino *et al.*, 2003; Pannell *et al.*, 2004) because their vegetative growth can be negatively affected. Herbicide efficacy is considered to depend on the herbicide dose (Navarrete *et al.*, 2000). Also, the establishment of vigorous and competitive crops (or denser stands) can lead to a reduction of the reproductive output (Monaghan, 1980; Izquierdo *et al.*, 2003). So, the seed production per individual can be rewritten as:

$$F = f\,(1-c_2)(1-c_3)/(1+a\,M_t) \tag{5}$$

where c_2 is the reduction of fecundity by herbicide sublethal effects and c_3 is the control of seed production by competitive crops. Then, total seed production in a pixel (S_t) is given by:

$$S_t = F\,M_t \tag{6}$$

2.2. Dispersal

At this point of the population model we include a dispersal event, which "disperses" the seeds produced in a pixel into the grid. Seed dispersal can be split in two separate phenomena, primary and secondary dispersal by combine harvesters. Equations describing seed dispersal as a function of the distance to the source were generated from experimental data previously reported by Blanco-Moreno *et al.* (2004), and had been modified to account for primary (natural) seed dispersal. Primary dispersal of *L. rigidum* is restricted in space and the amount of seeds is of lesser importance –about 6% of the total (Blanco-Moreno *et al.*, 2004)–. So, a *n* proportion of the seeds is dispersed with distances according to a normal distribution function centred on the pixel's midpoint and with no preferential direction (omnidirectional or isotropic):

$$Normal(\sigma_n) = (n)\left[\exp\left(-distance^2/2\sigma_n^2\right)/\sigma_n(2\pi)^{0.5}\right] \tag{7}$$

where σ_n is the shape parameter of the normal distribution function. σ_n was parameterised taking into account that half the seeds should be dispersed within a radius half the height of the mother plant (Cousens & Mortimer, 1995) after primary dispersal.

Dispersal pattern parallel to combines' movement can be described by a compound model (Howard *et al.*, 1991; Blanco-Moreno *et al.*, 2004), formed by a normal function centred slightly behind the point of introduction, and a negative exponential function from the point of introduction forwards. These functions were established using the following equations:

around the focus and backward direction of combine movement:

$$Normal(\sigma_l) = (p)(1-n)\left[\exp\left(-\left(distance_{parallel} - \mu\right)^2 \Big/ 2\sigma_l^2\right) \Big/ \sigma_l (2\pi)^{0.5}\right] \tag{8}$$

and forward the combine movement:

$$\begin{gathered} Normal(\sigma_l) + Exponential(\beta) = \\ (p)(1-n)\left[\exp\left(-\left(dist_{parallel} - \mu\right)^2 \Big/ 2\sigma_l^2\right) \Big/ \sigma_l (2\pi)^{0.5}\right] + (1-p)(1-n)\left[\exp\left(-dist_{parallel} \big/ \beta\right) \big/ \beta\right] \end{gathered} \tag{9}$$

where n is the proportion of seeds dispersed in the primary dispersal event, p is the proportion of seeds dispersed according to the normal distribution function, σ_l is the shape parameter of the normal function around the focal pixel, μ is the position parameter of the normal function and β is the shape parameter of the exponential. The σ_l and β values (shape parameters, see Table 1) are different from those offered by Blanco-Moreno *et al.* (2004). Our values are three fold higher than theirs, since they used them to compare the dispersal by two combine types in a design in which sampling was done at three meter intervals.

The lateral seed movement by combines were described using a normal distribution function:

$$Normal(\sigma_p) = (1-n)\left[\exp\left(-\left(distance_{perpendicular}\right)^2 \Big/ 2\sigma_p^2\right) \Big/ \sigma_p (2\pi)^{0.5}\right] \tag{10}$$

where σ_p is the shape parameter of the normal distribution function. This equation does not include any position parameter because the seed dispersal curve is assumed to be symmetrical and centred on the movement of combine. Lateral seed movement has been described here by a normal distribution function instead of a Cauchy (see Blanco-Moreno *et al.*, 2004), because although the Cauchy adequately describes previously reported experimental results of combine dispersal (Blanco-Moreno *et al.*, 2004), it yields non-sense results in simulations (lateral dispersal occasionally exceed longitudinal seed dispersal distance, results not shown).

Although the shape of dispersal curve can be different depending on the kind of combine harvester (Ballaré *et al.*, 1987b; Blanco-Moreno *et al.*, 2004), we’ll consider here only a standard combine, since the differences between combines’ dispersal are also associated with differences in many other management practices. The equations describing seed dispersal were included in the model to obtain series of random numbers which reproduced the dispersal of individual seeds in two dimensions. This could be criticised since an important fraction (up to 16%) of *L. rigidum* seeds are dispersed clustered in spikelets or spike fragments (Gill, 1996a), however the effect on dispersal distance can be considered minimal (Blanco-Moreno *et al.*, 2004).

2.3 Seed losses and seed bank

Nevertheless, not all seeds produced in a season are incorporated into the seed bank because they can be lost due to depredation, in a proportion l_1, or can be caught with the grain in the harvester or in specially designed carts (Walsh & Parker, 2002), in a fraction l_2. However, these losses occur at different moments. While l_1 is considered to affect all the seeds produced (all seeds are exposed to natural depredation), l_2 only acts on those seeds dispersed by the combine harvester. Primary dispersal by harvest time of *L. rigidum* is very restricted in space and the amount of seeds is of lesser importance (Blanco-Moreno *et al.*, 2004), but the seeds that are shed to the ground before harvest cannot be caught by combines, consequently cannot be dispersed by them. So, seed rain (R_t, seeds pixel^{-1}) can follow two alternate ways, primary dispersal:

$$R_{t\ primary} = S_t(1 - l_1) \tag{11}$$

And secondary dispersal by combine harvester:

$$R_{t\ secondary} = S_t(1 - l_1)(1 - l_2). \tag{12}$$

After dispersal phenomena, seeds are considered to enter in the seed bank, which can be expressed in terms of the previous years' seed bank remnants plus the new seeds incorporated into it:

$$SB_{t+1} = SB_t(1 - e)(1 - m) + R_{t\ (primary+secondary)} \tag{13}$$

where m is the natural decay of the seed bank in a year and e is the proportional seedling emergence from the seed bank.

However, this life cycle model can be disrupted under some management practices as crop rotation with a fallow season. Fallow is usually planned as a weed control measure as well as a way to store water and nitrogen (López Bellido *et al.*, 1996; Porter *et al.*, 1996; McGuire *et al.*, 1998). In the fallow year, *L. rigidum* seedling survivorship is very low because of the various tillage. Moreover, during fallow, seed dispersal as well as seed losses by combines do not take place. So, only the primary dispersal (equation 7) is considered to act over the whole pool of seeds.

2.4 Incorporation of stochasticity in demographic processes

Plant abundance in a pixel should be adjusted to obtain in integer values, since at low densities there should be some mechanism for local extinction. Perry (1988) found that some process of rounding to an integer was essential to prevent spurious artifactual results in population modelling. Furthermore, the fate of individuals is clearly a stochastic process, subject to unpredictable random effects. To adjust any life-stage (SB, Z, M) to an integer stochastically, we have followed the approach of Perry and González-Andújar (1993). They added to any of the population stages, denoted *N*, an uniform random number between zero and one, denoted *U*, and took the integer part of the result:

$$I = \text{int}(N + U)\,. \tag{14}$$

This ensures that any population stage *N* is rounded up or down to one of its enclosing integers, with probability according to its closeness to those respective integers (e.g. 3.25 is rounded down to 3 with a probability 0.75 and rounded up to 4 with probability 0.25).

2.5 Parameter estimation

Demographic parameter values used in the model have been taken from the work of González-Andújar and Fernández-Quintanilla (2004), who in turn obtained them from the literature (Taberner, 1996; Fernández-Quintanilla *et al.*, 2000; Izquierdo *et al.*, 2003) or estimated them from previously unpublished results. The effect of control measures on population size has been taken from various sources [for herbicidal action Navarrete *et al.* (2000), Monjardino *et al.* (2003) and Pannell *et al.* (2004); for seed catching efficacy Walsh (1996), Walsh and Parker (2002), Matthews (1996b) and Matthews *et al.* (1996a); for crop competition Izquierdo *et al.* (2003)]. A summary of the values used in the parameterisation of the model are shown in Table 1.

The effect of management practices on population size and rate of spread was assessed only for a restricted set of them; only some of the most commonly applied (yearly herbicide application at full rate and cereal–fallow rotation) and some of those avoiding herbicides (delayed seeding date, crop seeding rate increase and seed capture at harvest) were tested. Herbicide application at full rate was assumed to exert 90% reduction in seed production ($c_2 = 0.90$); the increase of crop seeding could reduce seed production of individual plants up to 50% ($c_3 = 0.5$); the seed capture at harvest was assumed to have a 60% efficiency ($l_2 = 0.6$). The delayed seeding was considered to destroy up to 65% of the emerging seedlings ($c_1 = 0.65$); and only 2‰ ($s = 0.002$)of the emerging seedlings is assumed to survive to maturity in the fallow period.

Some authors have hypothesised that the greatest long-term benefits could be achieved by the integration of various control options rather than by the application of individual tactics (Jones & Medd, 1997). To test this hypothesis we have simulated the long term spatial dynamics of *L. rigidum* under the two types of integrated management programs proposed by González-Andújar and Fernández-Quintanilla (2004). Those integrated programs (programs B and C) were compared with the most common management practice in most of Spain, the yearly application of herbicides at full-rate (Program A). Program B, which represents the economically optimal cropping system (continuous barley), integrates chemical and cultural control (herbicide at half rate –80% efficacy–, delayed seeding –60% control–, high crop density –50% reduction of seed production– and seed catching at harvest –with an estimated efficacy of 60%–). Program C represents a system in which chemical control has been completely substituted by different cultural management practices (barley-fallow rotation, delayed seeding –60% control– and high crop density –50% reduction of seed production–).

Every combination of parameter values was run five times to assess the variability in the simulation process, and results were averaged over the five runs. The model runs were carried over 30 years. This time-span is considerably longer than that taken by non-spatial models to reach the equilibrium density. It was chosen because preliminary trials indicated that it was enough to reach a stable population size and to occupy the area. All simulations were begun with an initial population of 10 seedlings in the central pixel (position 0,0). The number of seedlings was chosen to allow for a positive integer value after the application of the different control measures.

Table 1 Parameter values used in the spatial simulation model. Some parameters can have alternative values depending on the conditions imposed on the model.

Parameters		Symbol	Value
Emergence		e	0.64
Seedling survivorship (barley year)		s	0.76
Seedling survivorship (fallow year)		s	0.002
Fecundity		f	935
Seed losses (predation, standard harvest)		l_1	0.19
Seed losses (seed catching at harvest)		l_2	0.60
Seed bank mortality		m	0.84
Control by delayed seeding		c_1	0.65
Control by herbicides (full rate)		c_2	0.90
Control by herbicides (half rate)		c_2	0.80
Control by crop competition		c_3	0.50
Seed bank mortality		m	0.84
Primary dispersal: omnidirectional			
	fraction of seeds	n	0.06
	shape parameter	σ_n	0.52
Secondary dispersal: parallel to combine movement			
	fraction of seeds in the normal function	p	0.58
	normal function shape parameter	σ_l	1.70
	exponential function shape parameter	β	9.37
Secondary dispersal: perpendicular to combine movement			
	normal function shape parameter	σ_p	0.68

2.6 Sensitivity analysis

In order to assess the sensitivity of the model to parameter change, a sensitivity index (SI) was calculated according to the method proposed by Pannell (1997). It proceeds by identifying those parameters most subject to change or uncertainty, selecting minimum and maximum values of each of these parameters and applying the following formula:

$$SI = \left(D_{max} - D_{min}\right) / D_{max} \tag{15}$$

where D_{max} is the output measure when the parameter under examination is set at its maximum value and D_{min} is the output obtained with the minimum parameter value. A large SI indicates that a small variation in that parameter results in a large modification in the model output. The model output was examined in terms of mean patch density, which was defined as the mean density of all colonised pixels at the end of the simulation. A pixel was considered to have been colonised when it had at least one seed in the seed bank.

3. Results

3.1. Simulating the dynamics of *L. rigidum* population under no management

In general, population grew following a sigmoidal curve. The equilibrium density (mean ± SE) without management was about 2318.65 ± 16.71 seeds m^{-2} (Fig. 2A). This high density can be regarded as the carrying capacity of the environment under the specific conditions to which the simulation process is constrained. Under this conditions the spatial model needed about 11 years to fill the whole field (Fig. 2B). However, the maximum density found in the field was much higher (about 5804.47 seeds m^{-2}; 250.3% of the mean equilibrium density) and was more variable than the mean density. Maximum density is achieved earlier (4 years) than the equilibrium density (Fig. 2A).

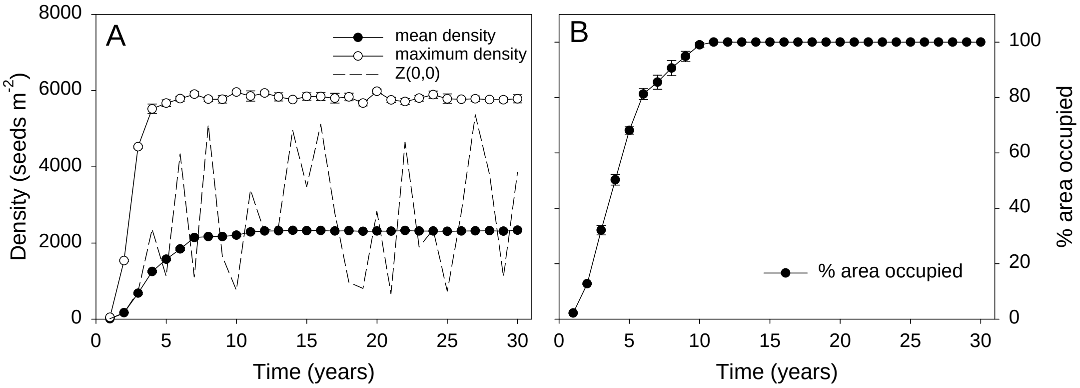

Fig. 2 Simulated population trends without management using the standard demographic parameter set. On the left there are measures of population size and variability; mean and maximum density are averages over five runs of the model. The dashed line indicates the predicted seed density at a given pixel (0,0) for a single simulation run. On the right there is the evolution of infested area, expressed as a percentage of the field area.

Moreover, the variability of the density in the field is high across space and time. The field presents a characteristic banded pattern that has already been documented for *L. rigidum* (Blanco-Moreno *et al.*, 2004), alternating high and low seed densities, from the second year onwards (Fig. 3). But this variability is not consistent from year to year. At any given location –see Fig. 2A, line corresponding to the pixel (0,0)– there is high variability in seed density and this variation is not periodic. The density at any location depends on the density at the neighbouring points and also on the passes of the combine, which can vary in the position and the direction from year to year.

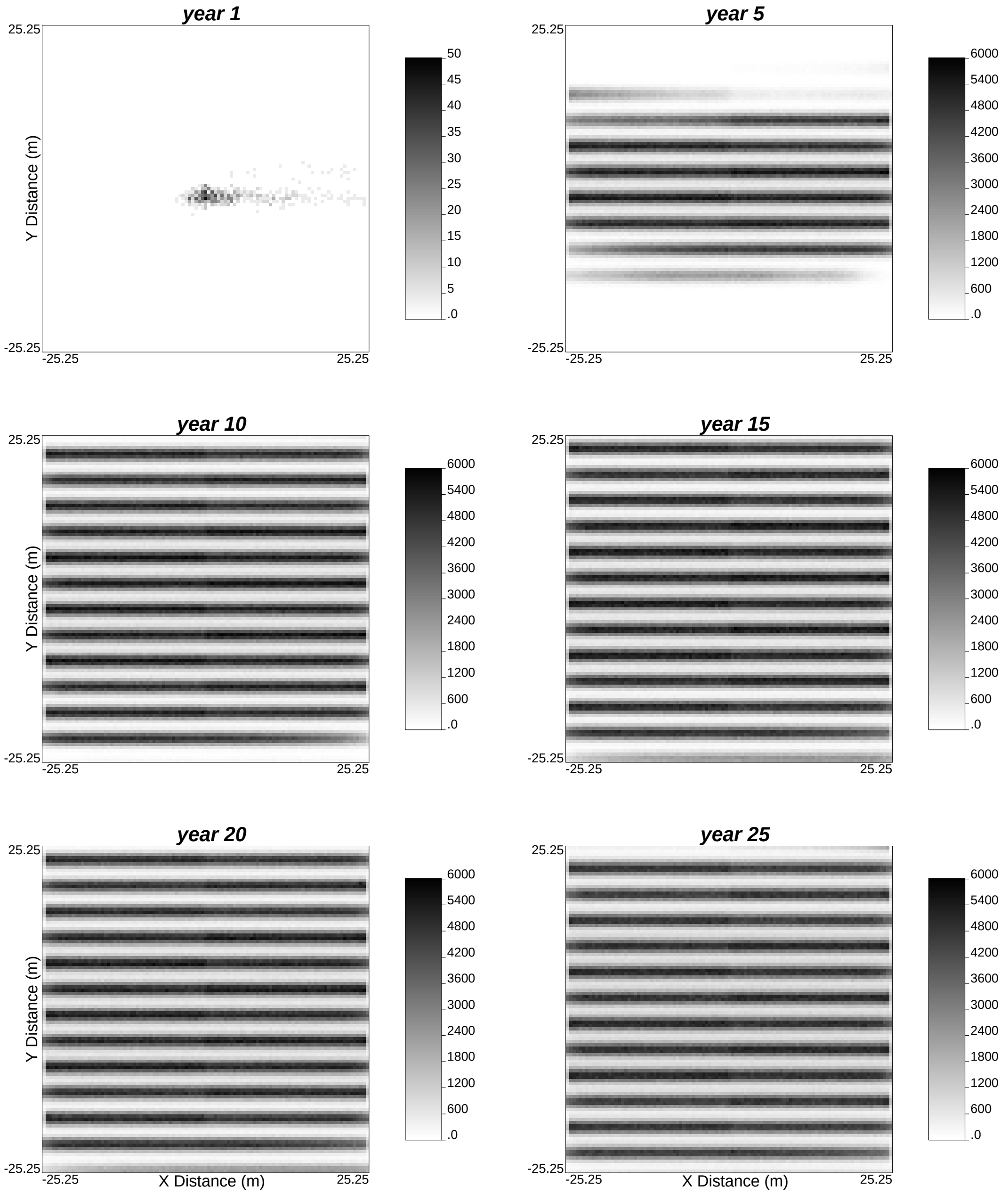

Fig. 3 Simulated seed population density maps without management using the standard demographic parameter set. Selected plots from one simulation run are shown. Scales are expressed in seeds m^{-2}. Note the different scale of seed densities among year 1 and all other years.

3.2. Sensitivity to demographic parameter variation

The sensitivity analysis show that effect of varying the demographic parameters on the model output was generally minor except for fecundity, which had a SI of 0.9989, and seed losses, which had a SI of -0.3866 (Table 2).

Table 2 Demography sensitivity analysis of the spatial dynamics simulation model in terms of total seed bank population. Model outputs are expressed in seeds m^{-2}.

Parameters	Maximum Value	(Model output)	Minimum Value	(Model output)	Sensitivity Index
Emergence (*e*)	0.8	(2192.77)	0.34	(2366.51)	-0.0792
Seedling survivorship (*s*)	1.0	(2258.85)	0.17	(2207.84)	0.0226
Fecundity (*f*)	1250	(3028.21)	7	(3.36)	0.9989
Seed losses (l_1)	0.35	(1809.61)	0.1	(2509.13)	-0.3866
Seed bank mortality (*m*)	0.89	(2214.48)	0.6	(2485.80)	-0.1225

When the lowest fecundity per plant (*f* = 7) is used, the mean population size is about 3.26 ± 0.030 seeds m^{-2} (Fig. 4) and does not stabilise and does not show a clear trend towards increase (or decrease). The area infested remains nearly constant (but erratic) within the time span used in simulation processes. *L. rigidum* seedling population undergoes extinction some year (results not shown) although it persists through the seed bank.

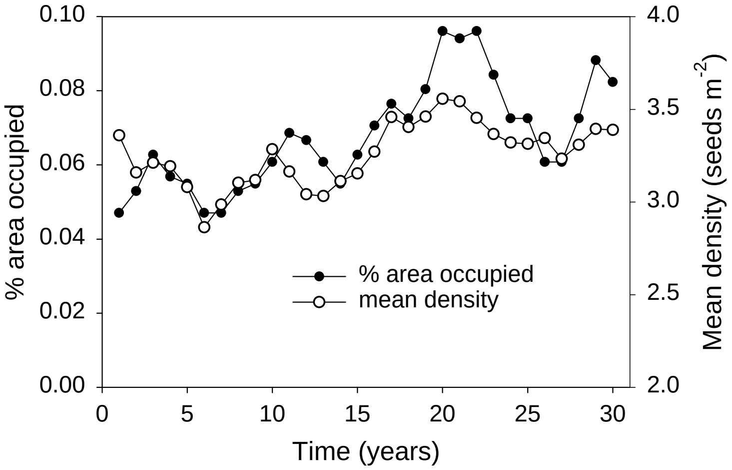

Fig. 4 Simulated population trends under no management measure using the lowest fecundity per plant (*f* = 7). Standard error values are not given to preserve clarity.

3.3. Assessing the effect of individual management practices

The effect of different management practices is shown in Fig. 5. Application of herbicide, with an expected efficacy of 90% (Fernández-Quintanilla *et al.*, 1998; Navarrete *et al.*, 2000), would result in 90.9% population reduction –estimated population 211.57 ± 0.115 seeds m^{-2}– (Fig. 5A). The herbicide also causes some delay in the expansion rate, although it does not prevent infestation of the whole field. The *L. rigidum* population needs 19 years (instead of 11 years with no control measure) to completely fill the field (Fig. 5B).

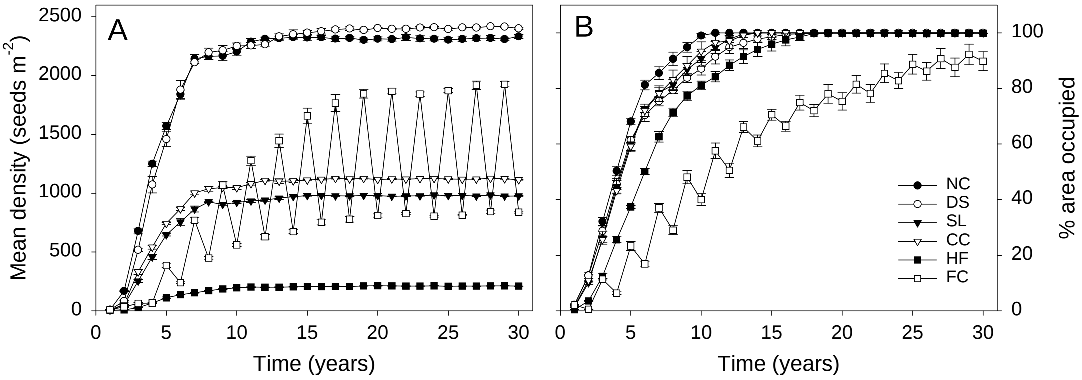

Fig. 5 Simulated population trends under some selected management practices. On the right there is the evolution of population mean density. NC represents the evolution under no management; DS means delayed seeding (c_1 = 0.65); SL represents seed catching at harvest (l_2 = 0.60); CC means control by competition from crop (c_3 = 0.50); HF means fecundity reduction by herbicides at full rate (c_4 = 0.90); FC represents cereal–fallow rotation with reduced seedling survival during the fallow period (s = 0.002). On the left there is the evolution of the occupied area, expressed as the percentage of the field area.

The delayed seeding with a control (c_1) of 0.65 does not achieve a reduction of the seed bank. The size of the seed bank at equilibrium is about 2404.08 ± 1.844 seeds m^{-2} (Fig. 5A). Although delayed seeding slightly increases the seed bank equilibrium density (3.58%), it delays the spread rate (Fig. 5B). The time to fill the whole area ranges from 13 to 20 years –there is a high variability in this parameter, average 15.8 years (Fig. 5B).

The seed catching at harvest results in a 57.81% reduction of the seed bank –the equilibrium density is about 978.81 ± 0.585 seeds m^{-2} (Fig. 5A)–. Under this control measure the simulated *L. rigidum* population takes from 13 to 14 years to infest the whole field (Fig. 5B).

The control through the establishment of competitive crops or the increase of stand density produces a long-term reduction of 52.4% of the population size. The seed bank under this control measure is about 1114.82 ± 2.774 seeds m^{-2}. However, the management of *L. rigidum* with competitive crops reduces only slightly the rate of spread within the field. The time to occupy the field is about 12 years (Fig. 5B).

The effect of fallow, however, is very different. Fallow reduces the *L. rigidum* population (1890.42 ± 17.736 seeds m^{-2} at the beginning of the fallow year, but only 825.26 ± 8.545 seeds m^{-2} in the cereal year, Fig. 5A). The effective reduction of the seedling population at the beginning of the cereal period is about 64.40%. The fallow–cereal rotation takes more than 30 years to completely fill the field, but we cannot define how much longer (Fig. 5B).

3.4. Assessing the effect of integrated management programs

The two integrated programs reduce the *L. rigidum* population, although there were differences between them in the density and the spread rate (Fig. 6). Program A is the same as using herbicides at full-rate (see section Assessing the effect of individual management practices). Program B achieved the highest density reduction, which kept the seed bank population at 71.97 ± 0.421 seeds m^{-2}, which means 4.86% of the density without any control. Program C kept the population size between the limits of 1801.08 ± 11.324 seeds m^{-2} in the fallow year and 494.36 ± 3.185 seeds m^{-2} in the cereal year, which means a 78.67% reduction at the beginning of the cereal year.

Spread restriction was fairly similar in both integrated tactics. Program B was more successful in restricting patch spread than program C only during the first years. During the cereal year in program C there was an increase of the area occupied. Neither of the two programs reached 100% infestation of the area before the 30 years.

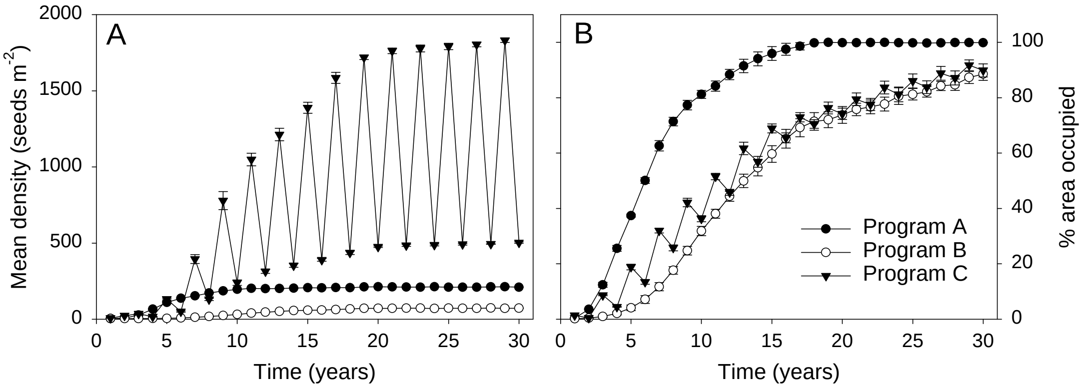

Fig. 6 Simulated population trends under different management practices (standard and integrated). On the right there is the evolution of population mean density. A is the "standard" herbicide regime. B and C are integrated programs (see text for details on the integrated practices). On the left there is the evolution of the occupied area (expressed as the percentage of the field area).

4. Discussion

4.1. The dynamics of *L. rigidum* population under no management

The integration of different sources of demographic information in weed population spatial dynamics models can help to understand the weed problem and address more effective management tactics. The construction of weed population models can help to identify critical gaps in the understanding of weed dynamics (Fernández-Quintanilla, 1988).

Our model predicts that *L. rigidum* without any control practice can build up massive seed banks, up to 2318.65 ± 16.71 seeds m^{-2}, which can cause severe yield reductions (Lemerle *et al.*, 1995; Cousens & Mokhtari, 1998; Lemerle *et al.*, 2001; Izquierdo *et al.*, 2003). But on the demographic basis there are some factors that could hinder the proper performance of the model. Previous demographic studies reported large differences in *L. rigidum* fecundity, with individual values ranging from 7 to 1250 seeds per mature plant (Monaghan, 1980; Recasens *et al.*, 1997; Fernández-Quintanilla *et al.*, 2000). Plant fecundity is largely determined by the interaction of biotic (e.g. crop cultivar and density, weed density) and environmental factors (Medd *et al.*, 1985;

Izquierdo *et al.*, 2003). Thus, it is necessary to identify the main factors that affect plant fecundity to prevent massive increase of *L. rigidum* populations.

One could argue that we do not need spatial models at all, since all of the previously exposed also stands for non-spatial population models. But our data indicate that a longer time span was needed for the stabilisation of populations with the spatial than with the non-spatial models. The non-spatial model needed four to five iterations (years) to achieve the equilibrium density, irrespective of the management practice or the density at equilibrium. In contrast, the time that the spatial model needed for stabilisation depends on the size of the field (results not shown) and on the management practices (see below).

The densities at equilibrium that we obtain are roughly the same as those obtained by the non-spatial model, indicating that the equilibrium densities are hardly affected by the imposition of dispersal on the model. The equilibrium density under no management was about 2318.65 ± 16.71 seeds m^{-2}, which is similar to the results of the non-spatial model (2357 seeds m^{-2}). In a sufficiently large area where most seeds produced are dispersed within it, dispersal should not affect the equilibrium density predicted by the spatial model.

However, in terms of evolution of weed population size there are some differences between the non-spatial and the spatial models; if seed dispersal is not taken into account, the non-spatial model systematically over-estimates the mean annual plant density compared to the spatial model. This model performance has been documented by Colbach and Sache (2001) for *Alopecurus myosuroides* Huds. The generation of density inequalities across the field owing to the dispersal process means that there are many areas of low density interspersed between high density areas. In fact, the very high density areas (well above the mean density predicted by the non-spatial model) are restricted to narrow bands across the field (Fig. 2).

Furthermore, our model outperforms non-spatial models because it takes into account stochasticity along with dispersal. At very low density these factors cannot be overlooked, since they could affect the fate of population. Take the example of the lowest fecundity used in simulations (f = 7). In this situation, if seed dispersal mechanisms are not affected by seed production, many pixels would receive only one seed. This seed can exclusively germinate, remain in the seed bank or die. Thus (local) population extinction is likely, because germination of the seed is not sure, and persistence in the seed bank into the next season is very unlikely. Moreover, if there is any exportation of seeds out of the field (e.g. by combines, see McCanny *et al.*, 1988) it would increase the risk of extinction. Only immigration could ensure population persistence, although at very low densities. Further examination over longer time spans and at landscape scale (cf. González-Andújar *et al.*, 2001b) could offer some insight into the persistence of weed populations at such critical size.

4.2. Assessing the effect of management practices

4.2.1. Population size

The different management reduce seedling population between 50% and 90% (results not shown). But the long term effect, assessed as the level of control achieved on the seed bank, is different and show a wider variation than seedlings.

The management measures that act on the seedling stage are expected to have a minor effect on the long term control of population size. Seedling emergence (SI = -0.0792) and seedling survivorship (SI = 0.0226) were likely to have almost no effect on the population dynamics of *L. rigidum* (except at very low population levels), since seed production is mainly regulated by density dependent phenomena, keeping seed production at high levels independently of weed density. Although only 2 ‰ ($s = 0.002$) of the seedlings is supposed to survive to produce seed in the fallow period (González-Andújar & Fernández-Quintanilla, 2004), the population produces enough seeds to replenish the seed bank during the cereal year.

Delayed seeding has been shown to be a good way to limit the seedling population during the cropping season, thus reducing yield losses by weed competition. Some studies in Australia and Spain indicate that delayed seeding can destroy as much as 80% of the seedlings, depending on the site and the season (Monaghan, 1980; Recasens *et al.*, 2001). If the aim is to minimise crop yield losses in a given season, delaying seeding can be a good strategy; but the size of the seed bank is not reduced, and consequently the threat for future harvests is not avoided. This practice causes a slight increase in the seed bank because the elimination of seedlings at the beginning of the cropping season ensures lower seedling density. Those seedlings have fewer competitors and thus produce more seed than they would have produced at high population density. However, the results of delayed seeding can be somewhat spurious because some authors have shown that late emerging individuals of *L. rigidum* can have lower fecundity (González-Andújar & Fernández-Quintanilla, 1991; Monjardino *et al.*, 2003). Some authors indicate an effective reduction (25%) after two years of delayed seeding (Matthews *et al.*, 1996b).The effect of emergence time on fecundity should be studied and incorporated to population models to assess the true effect of delayed seeding on the long term evolution of *L. rigidum* populations.

Other management practices such as herbicide application, the increase of crop competition and seed catching affect the incorporation of new seeds into the seed bank, through the reduction of fecundity or seed rain. Since the carry-over effect of the seed bank is expected to be very low [$(1-e)(1-m) = 0.054$], any reduction in seed shed will proportionally affect total seed bank.

The integrated programs reduced seed density at the beginning of the cropping season. The combination of distinct management practices is expected to affect the *L. rigidum* life-cycle at different stages, which can result in a large reduction of the population size. The integrated program C, which includes a fallow–cereal rotation, results in a higher seed density than herbicide application at the beginning of the cropping season. However, it proves to be effective to reduce the seedling population because delayed seeding is used in the cereal year as a control measure (results not shown). Program B, which combines herbicides at reduced dose with many cultural practices, obtains the highest *L. rigidum* population reduction.

4.2.2. Rate of spread

In general, the different management tactics have little effect on the rate of spread. Concerning the individual management tactics, only herbicide application at full rate and fallow delay the infestation of the whole field, and only fallow prevents complete infestation. Fallow takes almost 19 years to stabilise the high and low density oscillation limits, and it takes more than 30 years to infest the whole area. The fallow year represents a disruption of the expansion of patches because patch spread is mainly related to combines' secondary dispersal. Moreover, the high seedling mortality owing to the various tillage tend to reduce patch size during the fallow year, since most of the low density areas undergo local extinction.

Seed catching by combines seemed *a priori* a good tool to restrict patch spread. However, if the amount of dispersed seeds does not affect the dispersal pattern, the rate of infestation of the field is hardly affected, indicating that this rate does not depend on the quantity of seed available for dispersal. However, chaff collection at harvest could affect dispersal distance, since secondary dispersal mechanisms are the result of a combination of differential processing of chaff and straw that can lead to different dispersal patterns. Whether chaff collection has a distinct effect on dispersal remains to be examined.

Integrated programs were more successful in controlling patch expansion than individual practices alone. Integrated programs B and C prevent the saturation of the available space, although it is clear from the trajectories of infestation (Fig. 6B) that if the time-span is long enough complete infestation would occur.

Non-spatial weed population dynamics models only predict mean density. Non-spatial models do not contemplate the risk of infestation of uninfested field areas. Some authors have included rough predictions of seed dispersal from previously established weed patches to design "buffer" zones for patch spraying, accounting for the possibility of weed escape from patches (Rew *et al.*, 1997); they considered that a 4 m buffer was enough to restrict weed spread. Our predictions as well as data from other authors (Ballaré *et al.*, 1987b; McCanny & Cavers, 1988; Howard *et al.*, 1991) show that seed dispersal can considerably exceed such a distance, especially when dispersal by combines is taken into account. The dispersal behaviour of any weed should be well known in order to design useful management practices.

Our model predicts a relatively rapid infestation of the whole field, almost irrespective of the management tactics. Only a severe reduction of seed rain can avoid the infestation of the whole field. This should encourage further study of dispersal mechanisms. Greater attention needs to be given to the description of dispersal phenomena and to the analysis and modelling of the shape of dispersal distributions because rate of spread is more dependent on dispersal than on demographic processes. These results broadly agree with those of Woolcock and Cousens (2000), who worked out theoretically the implications of demography and dispersal on the spread of patches of four hypothetical weed types.

However, there are still more profound concerns about weed dispersal. Maxwell and Ghersa (1992), through the use of a simulation model, showed that in the long term seed dispersal may have a more important influence on crop yield than competition. The practical implication (as has been already pointed out) is that harvesters should be converted into weed seed “predators” rather than dispersal agents and thereby herbicide and mechanical weed control inputs could be reduced (Maxwell & Ghersa, 1992). However, our simulation results predict that, unless that seed capture at harvest could affect dispersal distance apart from affecting the quantity of dispersal units, the risk of invasion exists, and therefore a significant risk to future harvests.

Nevertheless, complex spatial simulation models do not ensure accurate prediction of weed density at discrete points. Small areas undergo a high variation that hinders the prediction of local seed and seedling densities (see the evolution of seed density at a given pixel in Fig. 2), thus limiting the value of complex models in recommending site-specific spraying (Colbach & Sache, 2001); however, they continue to be useful to simulate the effect of different cropping systems on the spread of weed patches and to choose those management practices minimising weed infestations and to propose suitable control measures.

4.3. Implications for pattern generation

Seed dispersal has been proposed to one of the causes of weed patchiness (Cardina *et al.*, 1997; Dieleman & Mortensen, 1999; Colbach *et al.*, 2000a; Cousens & Croft, 2000). The banded pattern of *L. rigidum* populations is clearly related to the seed dispersal by combines.

The banded pattern is caused by combines, but it is deeply affected by the quantity of seeds that are spontaneously dispersed before the crop harvest. If most seeds (e.g. more than 75%) are shed before crop harvest, the banded pattern does not appear (results not shown); however patches become elongated parallel to the direction of combine pass. Moreover, if previous years' seed bank remnants could have a high contribution to the seedling population the banded pattern could be faded away, masked by the superimposition of combine passes through years (Blanco-Moreno *et al.*, 2004). We have simulated the spatial evolution of *L. rigidum* populations with a minimal importance of primary seed shed (6%), which is supported by experimental results (Blanco-Moreno *et al.*, 2004). The quantity of seed that *L. rigidum* sheds before harvest depends on the temperature and rainfall conditions and also on the harvest date –the most is delayed the most seed is spontaneously shed (Matthews *et al.*, 1996a; Walsh, 1996; Walsh & Parker, 2002)–, so it could affect the conspicuousness of the banded pattern.

Nevertheless, the spatial population dynamics under different management tactics does not generate isolated patches. Wallinga *et al.* (2002) hypothesised that a true risk of a spread out pattern, without a closed advancing front but generating isolated "daughter" patches, would occur if dispersal distributions declined slower than exponentially. Our results agree with their theory, as there are almost closed fronts at the extremes of combine passes (see Fig. 3, year 5). In fact, although there is a closed front, the risk of colonisation far from the source plants exists because the rate of spread is relatively high. Weeds that retain some seed at harvest time represent an increasing concern, since they maximise the quantity of seed that can enter the combine, thus increasing the possibility of being carried far away from the mother plant.

Isolated patch formation is necessarily a conjunction of factors, which include not only demographic and dispersal phenomena. Although we have allowed for some stochasticity in demographic and dispersal processes, we have assumed that space is homogeneous, which might not be true (López-Granados *et al.*, 2002; Taylor *et al.*, 2003). Spatial environmental heterogeneity implies that weed performance might be different depending on topographical position within the field, thus leading to differences in the demography of the different patches (Piqueras *et al.*, 1999).

Moreover, we have assumed that biotic (inter and intraspecific competition) and environmental factors are constant, but these can vary from year to year (Cousens & Mokhtari, 1998; Cowan *et al.*, 1998; Lindquist *et al.*, 1999; Joernsgaard & Halmoe, 2003; Moechnig *et al.*, 2003). So, the effect of these biotic and abiotic factors on the demographic and dispersal parameters might also be different between years. In our model we have not varied the demographic parameters (*e*, *s*, *f*, *a*, l_1, *m*) from year to year or from pixel to pixel within a single run; although there are good reasons to suppose that they vary with the environment (Lush & Groves, 1981; Steadman *et al.*, 2003b; Steadman, 2004). This work should be extended to include such variation to offer an insight into the true spatial dynamics of weed and the importance of management tactics.

CHAPTER VI

GENERAL CONCLUSIONS

General Conclusions

The main conclusions emerging from this set of studies are presented below. Overall, the management of spatio–temporal variability of *Lolium rigidum* and *Avena sterilis* mixed communities in cereal crop fields has a favourable outlook. These two species have different life history traits that lead to different chances on their precision management.

1–The analysis of spatial distribution of a weed within a weed community at a given moment at a unique sampling scale does not offer an explanation of the spatial structure or dynamics of weed populations. The analysis of spatial structure at contrasting scales, of spatial stability and the joint analysis of all species in a weed community may alleviate some of the deficiencies of timeless monospecific spatial structure studies.

2–The spatial structure of the *L. rigidum* and *A. sterilis* at large is different than at fine scale. It indicates that the factors that affect the spatial structure of weed populations vary with the scale.

3–*A. sterilis* shows well defined and persistent patches which have a consistent spatial structure. These characteristics facilitate the site-specific management of its populations in cereal fields. However, *L. rigidum* populations do not present a consistent spatial and temporal structure, thus indicating it would be difficult to carry out site-specific management of its populations.

4–*A. sterilis* can replace *L. rigidum* in mixed communities in wheat fields under no herbicide pressure. In those places where *A. sterilis* populations are persistent over years it may successively replace *L. rigidum*, since *A. sterilis* is more competitive than *L. rigidum*.

5–The competitive effect of *L. rigidum* on wheat yield in mixed weed communities tends to be stable among locations within a field. However, *L. rigidum* does not show competitive stability across years; the effect of *L. rigidum* can vary largely depending on rainfall and temperature conditions during the growing season. The competitive effect of *A. sterilis* on wheat yield appears to be stable among locations as well as across years within a field.

6–*A. sterilis* is more competitive than *L. rigidum* in wheat fields, and this relationship is maintained across time and space. The high stability of *A. sterilis* competitive ability makes it a more suitable weed for precision agriculture than *L. rigidum*.

7–Combines can move *L. rigidum* seeds over long distances (> 18 m), although this is hardly relevant to the position stability of weed patches, since the dispersal modal distance is near to zero meters irrespective of the kind of combine (standard or with straw chopper) used. However, the long distance movement of some seeds may give rise to the extension of the patches, thus invading whole fields.

8–The shape of the dispersal curves by combines suggests that *L. rigidum* will display a spread pattern with a closed front that will move at a constant rate year-to-year, with no generation of satellite populations.

9–Seed dispersal by combine harvesters establishes the periodic spatial structure of *L. rigidum* populations at fine scale. Combines redistribute a fraction of *L. rigidum* seeds with chaff and straw causing a banded pattern of seeds and seedlings, with alternating high and low density bands. *A. sterilis* is not affected by combine harvesting since most seeds are shed before crop harvest; thus its populations do not show any banded pattern at fine scale.

10–Ploughing and residual seed bank from previous years do not affect the spatial structure of *L. rigidum* populations, since there is a spatial relationship between straw deposition in the preceding year and high seedling density areas.

11–The removal of harvest debris has a large potential for the management of *L. rigidum* populations in cereal fields. Chaff collection may be a good way to reduce the seed rain entering the seed bank for the following year; and thus reduce the generation of high density areas, which enable patch persistence despite the herbicide application. However, there is an important fraction of seeds that are dispersed jointly with straw and thus remain uncontrolled.

12–The incorporation of space into *L. rigidum* demographic models does not affect the equilibrium population density predicted by the models. However, non-spatial models tend to systematically overestimate the density, before the population reaches the equilibrium density. Thus non-spatial models predict faster population growth rates than spatial models do.

13–The spatial dynamics model predicts a high variability of *L. rigidum* population across space; the model generates interspersed high and low density bands, according to the pattern found in cereal fields. High and low density bands depend on the seed dispersal by the combine but not on previous years' population density.

14–The spatial dynamics simulation model cannot explain the generation of new isolated patches which is often detected in the field, since the spread pattern is continuous across space. Our results suggest that spatial and temporal variation of demographic parameters as well as variation in the efficacy of management practices play a leading role in the establishment of patchy weed distributions. The effect of this spatial and temporal variation should be studied to understand the patchy distribution observed in the field.

15–The spatial dynamics simulation model predicts a rapid spread of *L. rigidum* over the whole field in few years, almost irrespectively of the management practices. It indicates that the rate of spread does not depend on the demography of the population but only on the dispersal mechanisms of *L. rigidum*. Only the practices that minimise seed movements (i.e. fallow) or those that greatly reduce seed rain (more than 95%) can delay spread. Thus, the only effective way to reduce *L. rigidum* spread is to design management tactics that could reduce the dispersal distance along with the seed rain.

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